ECOLOGY OF PRINCE OF WALES SPRUCE GROUSE

by

Aleya R. Nelson

RECOMMENDED:

David Verbyla

Advisory Committee Co-Chair

Advisory Committee Co-Chair

Chair, Wildlife Program,
Department of Biology and Wildlife

APPROVED:

Dean, College of Natural Science and Mathematics

Dean of the Graduate School

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Date

ECOLOGY OF PRINCE OF WALES SPRUCE GROUSE

A

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Aleya R. Nelson, B.S.

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ABSTRACT

Recently, spruce grouse on Prince of Wales Island (POW) in southeast Alaska have been proposed as a separate subspecies. Furthermore, life-history of spruce grouse on POW, which is temperate coastal rainforest, varies sufficiently from birds in mainland areas, mostly boreal forest, to warrant specific management. Therefore, I examined the ecology of spruce grouse on POW to determine how timber harvest influences their survival and habitat selection and ultimately to provide recommendations for their conservation. During 2007-2009, we found that the greatest variation in survival probability was attributed to breeding status. The annual survival of non-breeding birds was 0.72±0.082 ($\hat{S}$±SE_S) while for breeding birds it was 0.08±0.099. Logging did not adequately predict survival, with no differences among habitats. Conversely, I found differences in selection among habitats. At the watershed scale, spruce grouse preferred unharvested forest. At both watershed and homerange scales, spruce grouse avoided edges and preferred roads. Road-related mortality was the largest known source of death. POW spruce grouse and mainland subspecies exhibit sufficiently different survival rates and habitat preference to warrant specific management. We recommend limited road closures during periods when POW spruce grouse are most vulnerable due to the high rates of mortality associated with this preferred habitat.

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INTRODUCTION

Information on survival rates of animals is critical to understanding how populations respond to ecosystem change (Lebreton et al. 1992). Survival rates are affected by both spatial and temporal variation in environmental factors. Generally, patterns of habitat selection reflect distinct survival benefits conferred with choice of habitat. To understand habitat selection of animals we must consider the life-history implications of such choices (Jones 2001). Therefore, it is important to measure fitness components associated with a habitat to provide insight into the adaptive significance of selection (Martin 1998) and for effective management decision-making (Pulliam et al. 1992).

The interaction between habitat selection and survival has not been adequately investigated for spruce grouse (*Falcipennis canadensis spp.*) though future modifications are projected for the boreal forest, which forms the majority of its range (Boag and Schroeder 1992). Deforestation from agriculture, logging, and industrial development are altering the boreal forest ecosystem (Hobson et al. 2002). Spruce grouse at the edge of their range, i.e., southeast Alaska, may also be affected by habitat modification, particularly because these smaller, edge populations are more vulnerable to stochastic factors (Caughley 1994, Lawton et al. 1994). In response to changes in the landscape of the Tongass National Forest in southeast Alaska through clearcut logging, a proposal for subspecies classification of spruce grouse (*Falcipennis canadensis isleibi*) on Prince of Wales Island (POW), and information needs regarding grouse in Alaska, I studied spruce grouse survival and habitat selection in response to forest management practices.

Survival of POW spruce grouse cannot be inferred from other spruce grouse. Across different species of grouse, survival commonly varies by sex, breeding, age, and season. Population vital rates appear to differ with respect to regional influences such as weather (Flanders-Wanner et al. 2004), habitat fragmentation and landscape development (Manzer and Hannon 2008), hunter harvest (Zwickel 1982), and pressure from predator communities (Devers et al. 2002). On POW, the extent to which these factors affect survival may be greater due to the substantial edge created by logging, increased access for hunters through an extensive road system, and inclement weather. In addition, POW spruce grouse habitat selection may also be affected by these factors.

The habitat of spruce grouse has been well-documented for birds across the boreal and montane forests of northern North America. Slight regional habitat differences exist, but spruce grouse are primarily a coniferous species. For instance, spruce grouse in Maine occupy the boreal-deciduous ecotone where highly fragmented coniferous forest is interceded by mixed-hardwood forest. Here they are found in small contiguous patches of spruce-fir forest (Allan 1985) and forested wetland refugia of black spruce-tamarack (Whitcomb et al. 1996). In Alberta, spruce grouse are commonly found in forests dominated by lodgepole pine (Schroeder and Boag 1991). Spruce grouse in Washington are found in mixed forest stands of sub-alpine Engelmann spruce-lodgepole pine (Ratti et al. 1984) and in the jack pine-spruce forests of northern Michigan (Robinson 1969). Spruce grouse are also found within the white/black spruce boreal forest across southcentral and interior Alaska (Aldrich 1963). These habitats vary greatly from the temperate coastal rainforest of southeast Alaska.

The primary objectives for this study were to understand how timber harvest influences the ecology of spruce grouse on POW in southeast Alaska because POW spruce grouse are proposed as a distinct subspecies and their use of temperate rainforest is unique over the range of the species. For Chapter 1, I determined survival rates and causes of mortality for spruce grouse in unharvested and harvested forest while examining the possible effects of other covariates on survival. I modeled survival of breeding and non-breeding birds and examined seasonal differences in survival. In Chapter 2, I described patterns of habitat use at the second-order (homerange selection) and third-order scales (use of areas within homerange; Johnson 1980). I was interested in how spruce grouse are using features created by timber harvest such as roads, forest edge, and successional forest within POW Island watersheds to delineate their homeranges. In addition, I examined how use of these features within homerange differs from use at the watershed level. A secondary objective was development of an effective sampling technique to consistently find spruce grouse and aid researchers in finding birds for future studies of grouse on POW Island. To do this, we compared detection rates among multiple sampling techniques: driving surveys, line transects with dogs, adaptive sampling, and occupancy sampling (included within Chapter 1). With both chapters, I examined what the survival implications were for specific habitat choices regarding timber harvest and how spruce grouse ecology on POW might vary from mainland populations of spruce grouse.

There is a contingent of interdisciplinary research on POW combining geology, fisheries, forestry, and wildlife to investigate forest dynamics. This study compliments

others including, harvest features associated with mortality risk for wolves (Person and Russell 2008); the relationship of POW flying squirrels to old-growth forest (Smith and Nichols 2003, Flaherty et al. 2010); the impact of pre-commercial thinning on birds (Dellasala et al. 1996) and small mammal communities; edge effects on avian nest survival (Sperry et al. 2008); interaction effects between karst and logging on salmon streams; social, ecological, and genetic dimensions of Sitka black-tail (Farmer et al. 2006, Brinkman et al. 2009, 2010); and classic studies of forest regeneration rates in temperate rainforest (Alaback 1982). My hope is that this research will contribute to the greater understanding of the effects of timber harvest in this unique island ecosystem and be considered within future decision frameworks regarding forest management practices.

CHAPTER 1. Survival of Prince of Wales Spruce Grouse in Southeast Alaska[1]

ABSTRACT

Prince of Wales spruce grouse (*Falcipennis canadensis isleibi*) are a potential conservation concern in southeast Alaska due to geographic isolation and recent alterations to forest habitats on islands within the Alexander Archipelago, where they are known to occur. In addition, these birds may receive a subspecies classification distinct from mainland populations. As a result, this study was conducted to learn more about spruce grouse population dynamics in temperate rainforest and the effects of timber harvest. During 2007-2008, we radio-marked 38 grouse to investigate how timber practices affected their mortality risk. We also examined how season, gender, and breeding status affect survival probability. Breeding status caused the most variation in survival probability. The annual survival of non-breeding birds was 0.72±0.082 ($\hat{S}$±SE_S) while for breeding birds it was 0.08±0.099. Survival for non-breeding birds was highest during the period spanning winter and spring, 0.93±0.089, compared to equivalent rates for summer and fall, 0.88±0.058. Effects of breeding lasted throughout the year, with non-breeding birds being about twice as likely to survive each season as breeding birds. Seasonal survival for breeding birds in winter-spring, 0.41±0.156, was similar to survival in summer and fall, 0.42±0.021. Timber harvest was not as important in predicting

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survival as breeding status, with no differences detected between habitat types. Road-related mortality (hunter harvest and vehicle strike) was the largest known source of death (42%) for spruce grouse followed by predation (25%) and unknown causes (25%). Our results show that the time when birds are breeding is the most critical period of survival and this investment in reproduction can have long-term implications. If survival of Prince of Wales spruce grouse is of concern and hunting has an additive effect on survival, we suggest temporarily closing select logging roads to allow broods to utilize the road network safely.

KEY WORDS survival probability, spruce grouse, temperate rainforest, breeding birds, logging, Prince of Wales Island, southeast Alaska

INTRODUCTION

The spruce grouse (*Falcipennis canadensis isleibi)* that inhabit Prince of Wales Island (POW) in southeast Alaska are of conservation interest for several reasons. First, spruce grouse abundance and life-history on POW and surrounding islands in the Alexander Archipelago is unknown. Mainland populations of spruce grouse occur mostly in boreal and montane forest habitats (Aldrich 1963, Schroeder and Boag 1991) and although these mainland populations have been studied (Ellison 1973, Ratti et al. 1984, Boag and Schroeder 1987, Whitcomb et al. 1996) it is unclear if their demography differs from island populations, which is temperate rainforest. Second, spruce grouse on POW Island were recently proposed as a separate subspecies, *Falcipennis canadensis isleibi,* based

upon morphological and genetic findings (Dickerman and Gustafson 1996, Barry and Tallmon 2010). Finally, POW Island has experienced high levels of public and private forest harvest (USDA Forest Service 2008*a* and USDA Forest Service 2008*b*). Approximately 13% of National Forest forested lands have been clearcut since the 1950's (USDA Forest Service 2008*b*), which results in various successional stands of uniform age. The forest regeneration rate is fast but understory vegetation peaks 15-20 years following clearcutting then declines with canopy closure around 25-35 years (Alaback 1982). Ensuing second-growth stands are characterized by dense overstory, high stem densities, and lack of understory vegetation (Harris 1974, Alaback 1982). Because of these concerns we initiated a study to estimate abundance and survival probability of POW spruce grouse and examine how habitat, grouse behavior and demography, and environment influenced survival.

In areas that undergo rapid landscape-level alteration, such as POW Island, a viable survey technique can help to detect changes in the abundance of a species. Spruce grouse are infrequently observed on POW Island and are considered rare. They rely on cryptic coloration and inhibited movement to avoid detection by predators and humans. However, they are occasionally detected gritting and feeding along the road system. The birds are reported to be opportunistically harvested when sighted during the hunting season. Their elusive nature may result in few sightings and influence the perception of scarcity or infrequent observation may reflect a true low abundance.

Our attempts to estimate abundance of spruce grouse were largely exploratory because few rigorous techniques have been developed specifically for estimating abundance of

arboreal grouse particularly when these birds are thought to be elusive or rare. Typically, spruce grouse are arboreal specialists spending a large portion of the year in trees. Therefore, sampling requires consideration of that proportion of the population that is unavailable to be sampled (i.e. off the ground) and the proportion that is available (i.e. on the ground, Thompson 2004). We tried to adapt some traditional survey methods such as line transects and also explored other techniques that have proven useful for rare species such as occupancy sampling (Mackenzie 2006).

The effect of timber harvest on survival was of particular interest because spruce grouse use a variety of habitats and these habitats have been greatly modified. Habitat fragmentation due to logging is negatively correlated with spruce grouse survival and occupancy of residual forest patches (Turcotte et al. 2000, Huggard 2003). Survival rates for other species of grouse such as sharp-tailed and ruffed grouse are also influenced by habitat alteration (Manzer and Hannon 2008, Tirpak et al. 2008). Boreal forest grouse in Scandinavia have lower breeding success in areas fragmented by clearcut logging due to the reduction in older forest availability that has safer nesting opportunities (Kurki et al. 2000).

Several explanations for decreases in survival associated with habitat alteration exist. One: direct effects such as reduction in habitat or habitat quality negatively affect survival and two: indirect effects such as road infrastructure introduce predators and provide hunting access. Tirpak et al. (2008) found that higher road densities affect survival of ruffed grouse at a landscape scale. Both blue grouse and ruffed grouse broods have been shown to select roads (Zwickel 1982, Tirpak et al. 2008) and may experience

greater mortality from increased predator and human encounters. However, forest edges and roads have also been shown to have a positive effect on survival. Tirpak et al. (2008) also found that ruffed grouse had increased survival at a local scale when they were associated with road networks while an increase in reproductive success in logged areas was documented for boreal forest grouse in Russia (Borchtchevski et al. 2003). In general, fragmentation from logging and road building can expose grouse to a variety of successional stands and forest edges, which can have important implications for survival.

The effects of habitat fragmentation on survival may vary seasonally. Spruce grouse exhibit short migrations between winter and breeding ranges, which appear to be habitat driven (Boag and Schroeder 1992). During winter, males and females are more likely to be found in dense conifer stands (Allan 1985). In addition to differences in habitat between winter and summer ranges, there are generally differences in survival between these periods. The impact of winter on grouse survival has been examined for multiple grouse species. Devers et al. (2002) found that survival rates of ruffed grouse in the Appalachian region were lowest in winter while Hannon et al. (2003) similarly documented lower survival rates during the fall/winter for willow ptarmigan in British Colombia. Ellison (1974) also found that survival rates were lowest in fall and winter for spruce grouse in south-central Alaska. However, Keppie (1979) did not think that fall and winter were significant contributors to decreased survival for spruce grouse in Alberta. This suggests that there may be regional differences in climate or habitat that affect the survival of spruce grouse over the winter.

During the summer, breeding spruce grouse hens prefer forests with open canopy and greater understory (McCourt et al. 1973, McLachlin 1970, and Hedberg 1980). Multiple studies have found that spruce grouse and other grouse hens have reduced survival during this period (Keppie 1979, Gutierrez et al. 2003, Tirpak et al. 2006, Hannon et al. 2003, Manzer and Hannon 2008). Tirpak et al. (2008) found that high quality brood habitat was an important component in survival of young ruffed grouse. Hens spending more time on the ground with broods may increase their exposure to predators. Also, there may be decreases in fitness that are associated with the high costs of reproduction that make females more vulnerable to harsh weather. In general, survival rates of male and female grouse usually differ with females tending toward lower survival (Keppie 1979 and 1987, Robinson 1980). However, season appears to have a greater influence on grouse survival than sex (Gutierrez et al. 2003, Tirpak et al. 2006, Manzer and Hannon 2008).

Within the POW Island ecosystem we hypothesized that spruce grouse would have seasonal habitat requisites and consequently exhibit seasonal and habitat differences in survival. We speculated that spruce grouse would have higher survival during the winter when they are primarily arboreal, display limited movement, and have protection from inclement weather. We expected the lowest survival during the summer and fall when females were actively breeding and birds were frequently foraging in the understory of the forest floor.

Our objectives for this study were to examine survival of POW spruce grouse under multiple timber harvest conditions, identify sources of mortality, and to compare sources of variation in survival among different environments and subspecies of spruce grouse.

STUDY AREA

POW Island is located at the southern tip of the Alexander Archipelago in southeast Alaska (Fig. 1). It is the third largest U.S. island at approximately 6900 $km^{2.}$ The majority of the island is within the Thorne Bay Ranger District of the Tongass National Forest. This is a heavily logged region of the island and an extensive logging road network (approximately 3600 km) has been established to facilitate timber harvest. POW Island has a maritime climate, influenced by the Pacific Ocean to the south and west of the Island and the warm water incursion of the Japanese Current. Average annual temperatures range between 4.7 and 10.7 degrees Celsius. Annual precipitation is generally greater than 250 cm, with October and November as the wettest months (Western Regional Climate Center 2009). Average annual snowfall is 101.25 cm with heavier snow typically occurring at higher elevations. Localized weather patterns are prominent and distributed across the island, resulting from rugged topography and ocean winds.

In addition to the temperate climate and high annual precipitation, an underlying karst substrate supports high forest productivity. POW was once the location of some of the largest trees in Alaska. Sitka spruce (*Picea sitchensis)*, western hemlock (*Tsuga heterophylla*), western redcedar (*Thuja plicata*) and Alaska cedar (*Chamaecyparis*

nootkatensis) comprise the megaflora of this coastal temperate rainforest ecosystem. Plants of the subcanopy and subshrub layers consist of shorepine (*Pinus contorta contorta*), red alder (*Alnus rubra*), Alaska blueberry (*Vaccinium alaskensis)*, red huckleberry (*Vaccinium parviflorum)*, crowberry (*Empetrum nigrum*), and bunchberry (*Cornus canadensis*). Common forbs in the understory are foam flower (*Tiarella trifoliate*) and five-leaved bramble (*Rubus pedatus*).

The high rates of forest productivity have led to substantial harvest activity within Tongass National Forest (TNF) lands across the island since the 1950's. Forty-one percent of the total timber harvest in the TNF has been on POW Island. Fifty-one percent of harvested forest in the TNF was from the high-volume old-growth (HVOG) category. However, 64% of harvested forest on POW was from HVOG, which is 28% of the original HVOG on POW. Overall, 21% of productive old-growth on POW has been logged, which is about 13% of its total public forested lands (USDA Forest Service 2008*a* and USDA Forest Service 2008*b*).

Willow ptarmigan (*Lagopus lagopus*), rock ptarmigan (*Lagopus mutus)*, northern goshawk *(Accipiter gentilis)*, marten (*Martes americana)*, northern flying-squirrel (*Glaucomys sabrinus),* Sitka black-tail deer (*Odocoileus hemionus sitkensis*), gray wolf (*Canis lupus)*, and black bear (*Ursus americanus)* also occur on POW Island. No other forest grouse occur on the island, although blue grouse occur on nearby islands in the archipelago and *F.c. franklinii* inhabit the mainland of British Colombia.

METHODS

Field Methods

We conducted intensive field work from March to August in 2007 and from May to October in 2008. We attempted to develop survey methods for spruce grouse to estimate abundance. We conducted counts along the road system. We drove logging and paved roads, during raining and rain-free periods. We varied the time of drives from 0500-2300 hours, with the majority of drives between 0700-1900 hours. Drives between locations of radio-collared birds comprised the majority of this sample when driving specifically for grouse was determined inefficient (1 sighting for every >1000km driven).

In addition to driving, we hiked transects with dogs in areas with historical and recent sightings as well as random areas with no grouse sightings. Recent grouse sightings were less than one week old while historical were generally within the last few years. We also used dogs to pursue immediate sightings transmitted from other field workers, generally reports from Forest Service employees by radio.

To obtain a sample of grouse for studies of survival and evaluating effectiveness of survey approaches, we captured birds using extensible noosing poles (Schroeder 1986, Zwickell and Bendell 1967) and fitted them with Model 1550 4.5 g necklace-style radio transmitters from *Advanced Telemetry Systems, Inc.*, Isanti, MN. We attempted to capture 20 birds each season. The transmitters did not have mortality switches and had an approximate battery life of 323 days. We checked birds approximately one week after the capture event and assumed no adverse transmitter effect if they survived the 7-day period. All subsequent relocations were visual with no triangulations. To test for

transmitter failure of birds that went off the air during the study, we first attempted to locate birds aerially to eliminate the possibility of wide dispersal and also checked within six POW villages for harvest by hunters. We made an effort to recapture and refit birds from 2007 for the 2008 season.

We relocated birds at least monthly to confirm survival and record habitat associations during the field seasons. Hens with broods were monitored with higher frequency to account for potentially greater rates of mortality during this sensitive period. We searched for nests during the breeding season, identified roosting areas, and observed conspecific interactions with radio-collared birds during tracking. During the off-season, USFS employees tracked birds 1-2 times to examine over-winter survival.

We categorized mortality as: hunter harvest, road strike, predation (mammalian/avian), natural causes, or unknown. Harvested birds were recovered from hunters or in pieces from the roadside. Birds that were found dead along roadsides, but intact, were attributed to vehicle strike. We distinguished between avian and mammalian predation based upon where the transmitter was found (e.g., tree/log, root wad), whether or not it was damaged (e.g., tooth marks), and how the carcass was consumed (e.g., plucking post). Birds that died from natural causes (potentially age, weather conditions, breeding stress, or disease) were found intact and in sheltered areas (root wad, under logs). We identified cause of death as unknown if only the transmitter was found and nothing conclusive could be inferred from its location.

We tested effectiveness of several survey techniques using known locations of radio-collared birds. We attempted to evaluate detection error of both dogs and observers

through occupancy sampling. To do this, we used a three-step process in which an independent observer first triangulated the radio-collared bird within a 0.25 km x 0.25 km grid cell. Then, a second independent observer, who did not know the location of the bird within the cell, would survey the cell for the grouse, either with or without a dog. Occupancy of a unit could be inferred from visual/auditory detection or upon discovering sign (e.g., feathers, scat, flush). Lastly, the initial observer would confirm that the bird was still in the unit if no detection was recorded. We deleted units from the sample in cases where the bird was not found in the cell afterwards. In addition to occupancy sampling, we evaluated detection error of dogs while tracking birds. In instances where hens did not have broods, we used dogs to detect presence of radio-collared birds.

Data Analysis

We used an extension of the Kaplan-Meier estimator that allowed for staggered entry into and right-censoring from the sample (Pollock et al. 1989). We input data using a daily nest survival format, consistent with ragged-entry telemetry data, in Program Mark, and estimated the daily survival rates of grouse (White and Burnham 1999).

We grouped birds according to year, season, and timber harvest type. We assigned season as winter, spring, summer, or fall but constrained winter and spring together because no mortality occurred during winter. Birds were assigned to a habitat type when relocated and we assumed that they remained in this habitat type between relocations during the field season when birds were intensively monitored. Habitat type was allocated to an unknown category during the off-season when birds were sporadically monitored. We assigned birds to unharvested, harvested, and unknown habitats. We

constrained edge habitat with harvested habitat due to relatively few relocations in edge habitat and because edge was ultimately a function of forest management. Unharvested forest comprised high-volume old-growth, low-volume scrub, and muskeg forest types. Harvested forest included varying stages of successional growth from clearcut to 30+ year old stands and often included pre-commercially thinned areas. We classified edge habitat as the area along the border of a managed forest stand, and buffered the line by 10 meters on either side. In addition, birds were also observed frequently along road sides. In these instances, habitat type was assigned according to the ambient forest. We only used the three general habitat categories to maintain sufficient sample sizes.

To classify seasonal survival, we divided the year into classic seasons. Winter occurred from December 22 to March 20; spring: March 21 to June 20; summer: June 21 to September 21; and fall: September 22 to December 21. We did this because there was no data on when the breeding season commenced for POW spruce grouse and in both years of the study there was snow on the ground into May. In addition, the temperate rainforest may affect the natural history of these grouse differently than boreal spruce grouse.

We used three individual covariates associated with each bird: sex, breeding status, and age since marking. We classified a bird as "breeding" if it was either nesting or attending chicks. Hens with brood patches were not included as breeding birds unless nesting activity or chicks were documented. Consequently, non-breeding birds included not only males, but also females without documented breeding activity and females

pre- and post-breeding. This allowed the survival rates of breeding hens to vary after they returned to a non-breeding state, i.e. broods dispersed. We used the covariate age since marking as an age approximation to account for the number of days that an individual bird had been marked. This allowed for any potential survival benefits associated increasing age of the bird.

We developed a candidate model set where survival was described as a function of year, season, and habitat type. We examined the effect that individual covariates breeding status, sex, and age since marking had on survival probability. We varied the effect of breeding status to be constant across seasons, to affect survival differently during winter-spring than summer-fall periods, or to only influence survival in summer-fall – largely the period of year when breeding activity was documented. In addition, we examined interactions between breeding status and timber harvest as well as between breeding status and age since marking. Other models included variation in survival between sexes not related to breeding condition and year-specific survival. Lastly, we tested the effect that 3 seasons had on survival: winter-spring, summer, and fall as well as the effect of these seasons at the mean breeding status.

We used Akaike Information Criterion, AICc, to select among competing models (Burnham and Anderson 2002). We model-averaged derived estimates across the candidate model set to incorporate model selection uncertainty (Burnham and Anderson 2002). We derived specific estimates of annual or seasonal survival from estimates of daily survival probability by raising daily survival to the appropriate power (length of the

period of interest). Standard errors for derived estimates were calculated using the delta method (Seber 1982).

RESULTS

Surveys

We encountered 64 spruce grouse through driving surveys (30), investigating reports (15), and tracking marked birds (19). Thirty of these were found through driving surveys with one bird sighted for every 1,130±232 km driven. Encounters were more frequent on logging roads at 1:548±106 km than paved roads at 1:4914±82 km. In addition, driving during rain-free periods increased the chances of encounter. We had 1:779±162 km birds sighted during rain-free periods and 1:4,291±82 km sighted while it was raining. Lastly, time of year influenced the number of grouse encountered while driving. We had the greatest number of sightings per effort in September and October with 1:677 km and 1:598 km, respectively.

We located 12 grouse immediately following reports by radio (n=18). Six of these were found while hiking without a dog (n=9), 3 while hiking with a dog (n=6), and 3 while the reporter remained within eye contact of the bird (n=3). In addition, we investigated 22 sightings that were greater than ½ day old ($\bar{x}$=2 days). We recovered 3 while hiking with a dog (n=20). No grouse were found hiking random transects in a variety of habitats with a dog (n=21).

For studies of survival and occupancy sampling, we captured 19 birds in 2007 and 19 birds in 2008. Captures occurred from April to October with the majority of bird caught

during June. There were a total of 26 females and 12 males in the sample. We disproportionately captured hen with chicks (42%) to just females and males. Throughout the study a total of 12 birds died; 3 from hunter harvest, 3 from predation, 3 from unknown causes, 2 from road strike, and 1 from natural causes. We documented nesting activity from May 14 to July 1 and hens attending chicks until October 6.

Through tracking radio-collared grouse, we encountered 19 unmarked birds in 297 relocations. Thirteen of these were in the immediate vicinity of the radio-collared bird while 6 were further than 50 meters from the grouse. Of these, we located 3 using dogs (n=3). The greatest number of these encounters occurred in October, or 1 unmarked bird for every 5 relocations of marked birds.

Rates of detection, evaluated through occupancy sampling, were less than 30% for both dogs and observers. Out of 20 0.25 x 0.25 km units surveyed with a dog, we detected spruce grouse presence 25% of the time. In 14 units surveyed without a dog, we detected spruce grouse 29% of the time. Detection using dogs while radio-tracking, 46% (n=69), was higher than rates associated with occupancy sampling.

Survival

The best approximating model (AIC_c weight=0.391) of survival included variation between seasons; summer/fall (β=6.46) and winter/spring (β=25.84), and breeding status; summer/fall (β=-1.84) and winter/spring (β=-20.807, Table 1). There was less support (model likelihood <0.42) for a model with differences between seasons as described above, but constant effect of breeding status (AIC_c weight=0.164) across seasons; a model with differences in survival among three primary seasons (winter/spring, summer,

and fall) with the additive effect of breeding status (AIC_c weight=0.081); a model specifying days since marking and the additive effect of breeding status (AIC_c weight=0.104), and a model with breeding status as the only predictor of survival (AIC_c weight=0.143).

Overall, models that included the effect of breeding status on survival accounted for 99% of the support in the data. The influence of sex on survival was not as important as breeding status. In fact, there was 338 times more support in the data for differences in survival between breeding and non-breeding birds as there was for differences between male and female birds. Breeding birds, ($\hat{S}\pm SE_S$, 0.08±0.099) had lower survival than non-breeding birds (0.72±0.082). This was consistent across seasons. The constrained season winter/spring had the highest rates of survival for all birds (Figure 2). Even though this portion of the year was twice as long as the other seasons, non-breeding birds had the highest rates of survival during this period, 0.93±0.089. Non-breeding birds were more than twice as likely as breeding birds, 0.41±0.156, to survive through winter-spring. Survival of breeding birds was 0.42±0.021 during the summer and 0.43±0.020 during the fall. Non-breeding birds were twice as likely to survive throughout summer, 0.88±0.058, and fall, 0.88±0.057, as breeding birds.

Timber harvest activity was not an important predictor of survival, with 4% of the support in the data, even when breeding status was considered (AIC_c weight=0.0269). The annual survival probability for breeding birds, 0.09±0.108, was 8 times lower non-breeding birds, 0.72±0.091 and both were equal in unharvested and harvested categories. Unknown habitat, or the unclassified habitat a bird occupied between field seasons, also

had comparable rates of survival for breeding and non-breeding birds, 0.09±0.109 and 0.71±0.090, respectively (Fig. 2).

DISCUSSION

Surveys

The survey technique through which we encountered the greatest number of birds was driving counts. However, this did not prove to be efficient per unit effort and birds found during driving were mainly sighted during subsequent in-transit travel. Several suggestions based upon our findings can be provided that may increase efficiency. Driving on logging or gravel roads was more conducive to finding birds. In addition, rain-free periods were more productive than rainy periods. We recommend combining searching during rain-free periods with driving on logging roads. Further, conducting driving surveys during the fall, particularly October, when the population is at its highest may yield the best results. October also proved to be a productive month for finding unmarked birds in association with radio-collared birds. Overall, dogs improved encounter rates for birds. However, rates of detection during occupancy sampling with dogs were not high enough to justify applying the technique to a landscape scale to estimate abundance.

Survival

We found differences in the survival rates of breeding and non-breeding birds. In general, non-breeding birds were over twice as likely to survive each of the winter-spring, summer, and fall seasons. Overall, non-breeding birds were 10 times more likely to survive an entire year than hens that nested or had broods during spring, summer, or fall months. This finding is consistent in studies with spruce grouse and among grouse species (Keppie 1979; Gutierrez et al. 2003; Tirpak et al. 2006; Manzer and Hannon 2008).

The reproductive season of spruce grouse on POW appears to vary slightly from other grouse and subspecies of spruce grouse. Breeding seasons usually occur from April-August with nesting concentrated in May and dispersal in September (Smyth and Boag 1984, Keppie 1979). We found evidence of nesting activity from May 14 to July 1. Hens brooded chicks as late as October 6 before we observed dispersal of young. Possibly due to an extended or delayed reproductive season on POW, breeding status was a more important predictor of survival than summer or fall, the actual breeding season. This may be attributed to survival of hens increasing after chicks have fledged or died and nests have failed.

We also found large differences in winter/spring survival for breeding and non-breeding birds. Generally, research has shown that differences exist between over-winter and breeding season survival (Ellison 1974, Keppie 1979). We not only found seasonal differences, but also that depending on whether or not a bird bred had an effect on its survival in the winter-spring season. More specifically, the impact of breeding on

survival lasted throughout the whole year. This suggests that there are long-term consequences to reproduction that reduce fitness of grouse annually.

Survival rates of POW spruce grouse in this study during the winter-spring time period differed from what Ellison (1974) found for spruce grouse in south-central Alaska. He found the lowest rates of survival over-winter, which could indicate that there are different environmental forces affecting the seasonal survival of both breeding and non-breeding birds on POW Island. The mean annual survival rate of POW spruce grouse, 0.39, is lower than *F.c. franklinii* populations in southwestern Alberta, 0.68 (Boag et al. 1979, Keppie 1979), and *F.c. canadensis* populations in Michigan, 0.48 (Robinson 1980), and New Brunswick, 0.47 (Keppie 1987), but higher than *F.c. canadensis* populations in south-central Alaska, 0.30 (Ellison 1974).

We did not find differences in survival between different types of forest harvest. In fact, annual survival rates among unharvested, harvested, and unknown habitats were equivalent for both breeding and non-breeding birds. However, birds did not usually exclusively use a single forest type. This suggests that usage of a variety of habitats throughout the year, for example, switching habitat seasonally, could be a strategy to maximize survival. We hypothesized that survival rates would be highest for unharvested forest and found lower survival than expected. However, if breeding hens select unharvested forest during the summer as brood habitat their lower rates of survival during this period could underestimate survival in unharvested forest. However, we did not detect this expected difference among habitat types for non-breeding birds either. We

did examine the effect of habitat type in specific seasons, but found that season was a more important predictor of survival than harvest.

The impact of forest edges on survival was not conclusive in this study. We infrequently relocated birds along managed edges and did not have enough data to draw conclusions about this habitat type. However, with 13% of public forested lands harvested on POW Island and substantial road building to support the fragmentation, birds were likely encountering forest edges at greater rates than we were documenting. Tirpak et al. (2008) found that ruffed grouse broods selected roads and had small survival benefits when associated with forest edges though these were mitigated by negative effects at the landscape scale. Heavier harvest of blue grouse with young also occurs along roadways in British Colombia (Zwickel 1982). Managed edge is not the only edge type of significance on POW Island. Unproductive old-growth and low-volume old-growth contain a high number of muskegs that usually have a distinct edge associated with them. These are areas in temperate rainforest that have poor drainage and result in moderate clearings with substantial berry crops. We documented spruce grouse using areas in and alongside muskegs, but classified this habitat as unharvested due to data limitations. Edge habitat usually offered some degree of cover with ample food. Its usage may have been a compromise between predator avoidance and foraging opportunity, conferring a distinct survival benefit. However, we were not able to investigate edge effect sufficiently in this study.

Limited information is available for grouse that inhabit temperate coastal rainforest. This study marks the first investigation of population dynamics for spruce grouse on

POW Island and for grouse in southeast Alaska. In addition, seasonal survival rates associated with habitat type for spruce grouse and the effect of breeding on long-term survival have not been documented. Overall, our results suggest that POW spruce grouse survival differs from other subspecies of spruce grouse and that the environment of POW Island may have unique survival implications.

Demographic rates for POW spruce grouse vary seasonally but are most divergent between breeding and non-breeding birds. To manage for survival of spruce grouse on POW Island, our results suggest that the period when hens are attending chicks is the most critical period for survival. Currently, hunting season begins August 1, which preceded chick dispersal in our study. In addition, most birds are opportunistically harvested along roads. Other sources of mortality, such as road strikes, cannot be easily managed. Essentially, there are few areas on the northern half of POW that spruce grouse are not within one kilometer of a road. To create a portion of the population that isn't exposed to opportunistic hunting and vehicle strikes during the breeding season would require road closure. Therefore, if survival of spruce grouse is of concern and hunting has an additive effect on survival, it may be beneficial to allow broods to utilize the road network safely through temporary and select closure of logging roads.

In addition to short seasonal closures, there may be room for considering grouse requisites, such as areas of high use or preferred habitats, in ongoing permanent road closures. The TNF was recently awarded economic stimulus funds through the American Recovery and Reinvestment Act (2009, Pub.L. 111-5) for road maintenance and decommissioning. The Forest Service is seeking to close 40% of open roads on POW

Island to reduce annual repair costs. The process of selecting roads for closure involves analysis of resource availability and levels of public access. We suggest identifying areas of high grouse use to inform conditions for road closure.

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Table 1. Candidate model set and model selection results for variables predicting survival of spruce grouse on Prince of Wales Island, AK, USA, 2007-2009.

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Num. Par	Deviance
S (2 season+different BNB)	92.737	0	0.39127	1	3	86.7324
S (2 season+BNB)	94.4748	1.7378	0.1641	0.4194	3	88.4703
S (BNB)	94.7489	2.0119	0.14309	0.3657	2	90.7467
S (ASM+BNB)	95.3754	2.6384	0.10461	0.2674	3	89.3709
S (3 season+BNB)	95.8673	3.1303	0.0818	0.2091	4	87.8597
S (ASM*BNB)	97.0343	4.2973	0.04564	0.1166	4	89.0268
S (2 season+summer/fall BNB)	97.4755	4.7385	0.0366	0.0935	3	91.4709
S (harvest+BNB)	98.0918	5.3548	0.0269	0.0687	4	90.0842
S (ASM)	103.9424	11.2054	0.00144	0.0037	2	99.9402
S (2 season)	104.0116	11.2746	0.00139	0.0036	2	100.0094
S (2 season+sex)	104.9246	12.1876	0.00088	0.0022	3	98.92
S (3 season)	105.4089	12.6719	0.00069	0.0018	3	99.4043
S	105.456	12.719	0.00068	0.0017	1	103.4553
S (sex)	106.3861	13.6491	0.00043	0.0011	2	102.3839
S (harvest)	106.7831	14.0461	0.00035	0.0009	3	100.7786
S (year)	108.8051	16.0681	0.00013	0.0003	3	102.8005

Note: Groups: **2 season**=winter/spring and summer/fall, **3 Season**=winter/spring, summer, and fall, **Harvest**= unharvested, harvested, and unknown. Individual Covariates: **BNB**=breeding and non-breeding, **ASM**=cumulative age since marking, **Sex**=male and female. Model Relationships: '*'=interaction, '+'=additive.

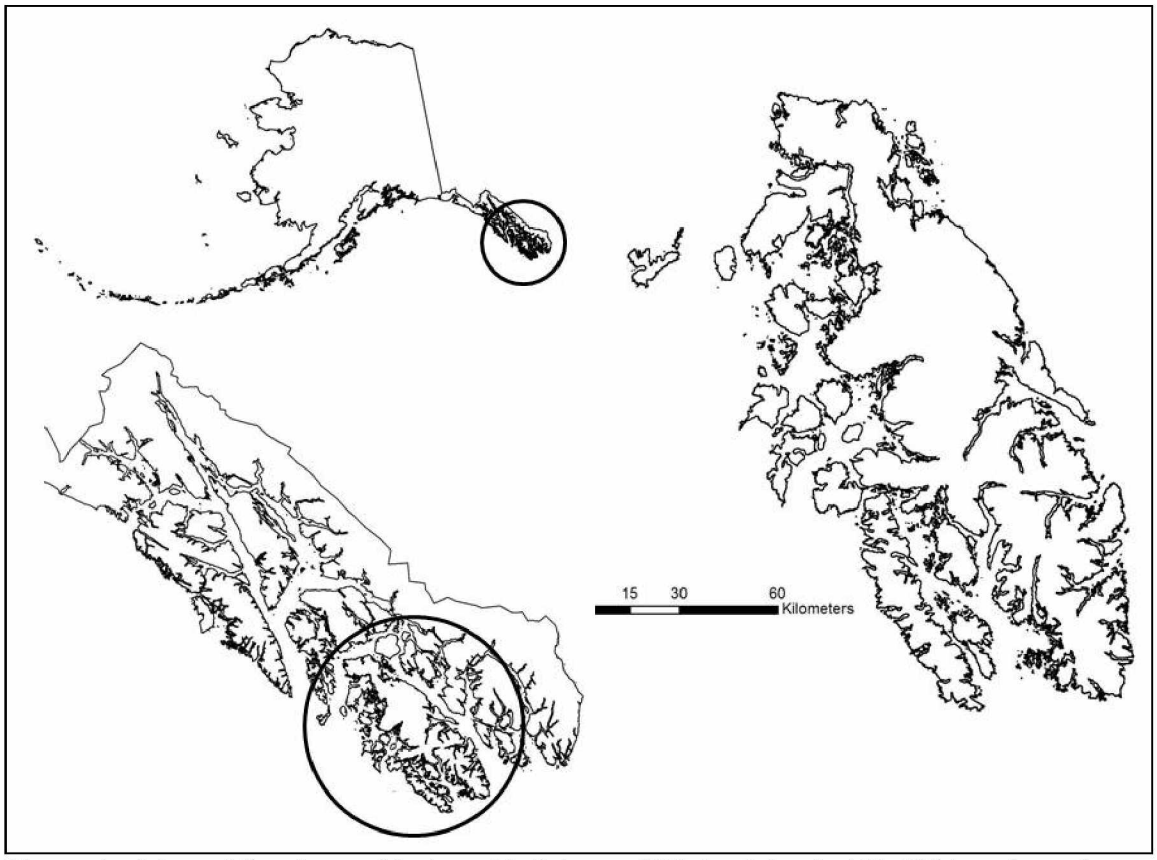

Figure 1. Map of Southeast Alaska with Prince of Wales Island, AK, USA, enlarged at lower left. The study area was mostly confined to the northern half of the island (AK-DNR 1998, Southeast Alaska GIS Library 2009).

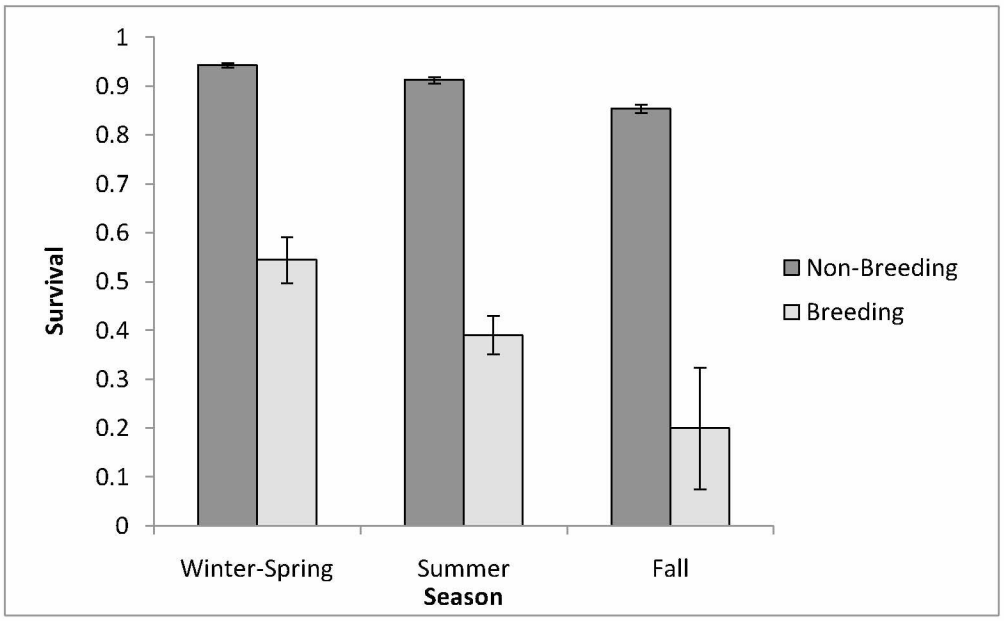

Figure 2. Seasonal survival estimates for non-breeding and breeding birds on Prince of Wales Island, AK, USA. Estimates are from model, $S=\beta_0+\beta_1(3\ season)+\beta_2(BNB)$.

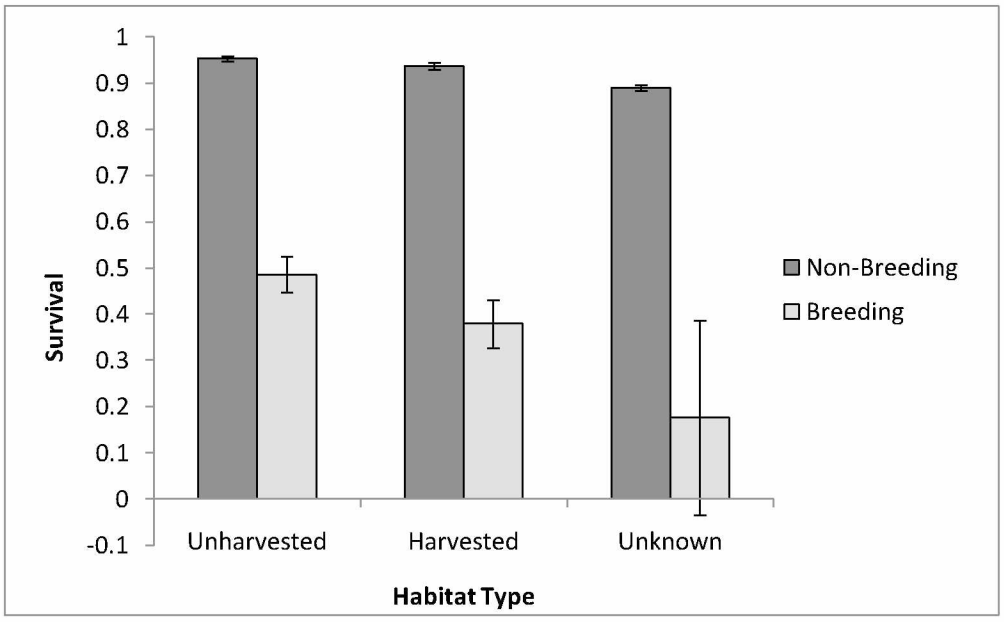

Figure 3. Seasonal survival estimates for 90-day interval survival of non-breeding and breeding birds across habitat type on Prince of Wales Island, AK, USA. Estimates are from model, $S=\beta_0+\beta_1(harvest)+\beta_2(BNB)$.

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CHAPTER 2. Habitat Selection by Prince of Wales Spruce Grouse in Intensively Logged Coastal Temperate Rainforest[2]

ABSTRACT

Habitat preferences have been well-documented for mainland populations of spruce grouse across northern North America. However, the climate and topography of southeast Alaska varies dramatically from these other areas occupied by spruce grouse. Spruce grouse in southeast Alaska, *Falcipennis canadensis isleibi,* are of much interest because they are believed to be rare and their habitats have been greatly altered by forest management practices, particularly on Prince of Wales (POW) Island. We investigated habitat selection of spruce grouse at multiple spatial scales on POW Island, placement of homerange within watersheds (2nd order selection) and use of sites within homerange (3rd order selection). We examined if spruce grouse are old-growth obligates or if there is a degree of seasonal selection for harvested forests. At the watershed scale, spruce grouse preferred unharvested to harvested forest. At both spatial scales, spruce grouse were less likely to be found near managed forest edges, but were found in close association with roads, most of which were created to support logging activities. We found evidence for both seasonal and brood-habitat selection. Habitat relationships were more defined

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during the summer and for non-breeding birds. Spruce grouse on POW Island had stronger 2nd order than 3rd order selection. Stronger relationships at the watershed level may be due to the importance of homerange placement with respect to limited habitat on the island and territory overlap. Grouse place their homeranges in areas with access to large patches of contiguous old-growth habitat, but that are within short distances to roads. Once their homerange is established, they may make more use of available habitats that include harvested forest.

KEY WORDS habitat selection, spruce grouse, logging, Prince of Wales Island, southeast Alaska

INTRODUCTION

Most spruce grouse (*Falcipennis canadensis spp.*) inhabit the boreal and cordilleran forests of northern North America (Boag and Shroeder 1992, Aldrich 1963). They also occur within coniferous forests in Maine and the Great Lake provinces and states of Ontario, Quebec, Michigan, Wisconsin, and Minnesota. Habitat preferences have been well-documented for these mainland populations (Huggard 2003, Whitcomb et al 1996*a*). However, the habitat needs of a recently described subspecies of spruce grouse occupying temperate coastal rainforest on the islands of the Alexander Archipelago in southeast Alaska (Barry and Tallmon 2010, Dickerman and Gustafson 1996) are not well known. These grouse, *Falcipennis canadensis isleibi,* are of much interest because they

are believed to be rare and their habitats have been greatly altered by forest management practices, particularly on Prince of Wales Island (POW).

POW spruce grouse must have specific and yet undescribed requisites to maximize their fitness in this unique environment if they occupied the area long enough to differentiate from mainland populations. However, these adaptations may be modified in an environment supporting timber harvest. Alteration of habitats may influence the distribution and frequency of use or shift habitat relationships completely. We studied habitat selection of POW spruce grouse in an environment shaped by logging.

The objectives of our study were to examine habitat selection at multiple spatial scales; to identify homerange selection in the landscape and then selection of sites within an individual bird's homerange. We examined if spruce grouse are old-growth obligates or if there is a degree of seasonal selection for harvested forests at both scales. Further we examined differences in habitat selection between breeding and non-breeding birds.

We used results from studies of spruce grouse at mainland sites to develop hypotheses about habitat selection of *F.c. isleibi* and how habitat use on POW Island may be affected by logging, season, and breeding activities. Within mainland landscapes spruce grouse prefer coniferous or mixed-coniferous areas and are usually associated with wet lowland forest (Whitcomb et al. 1996*b*), patch openings and edges (Robinson 1969), burns (Ellison 1973 and 1975), and successional forest (Schroeder and Boag 1991). In addition, their habitats are subject to a consistent fire regime. The climate and topography of southeast Alaska varies dramatically from these other areas occupied by spruce grouse. POW is historically productive old-growth rainforest with hydric

muskegs. Fire is virtually non-existent and spruce grouse are exposed to almost continuous precipitation. POW Island also undergoes large-scale landscape change through clearcut logging. We hypothesized that spruce grouse on POW would use openings, edges, and successional forest created by logging in a manner similar to these habitat types created by fire in mainland regions.

Spruce grouse on mainland sites also exhibit seasonal selection. Allan (1985) found that spruce grouse prefer different forest densities (# of trees/ha) among seasons. Spruce grouse are increasingly arboreal throughout the winter and subsist primarily on conifer needles (Keppie 1979, Ellison 1966). During winter, males and females are more likely to be found in dense conifer stands (Allan 1985). Conversely, their summer diet consists of berries, forbs, and herbs from the forest understory (Pendergast and Boag 1970, De Franceschi and Boag 1991). During summer breeding females preferred forests with open canopy and greater understory (Allan 1985). We predicted that second-growth forest on POW Island is representative of the denser conifer stands found on mainland sites and would be a preferred habitat type during the winter for abundant food and protective cover. Unharvested forest, which typically has a more developed understory, i.e., ample berry crop, good herbaceous cover, may be important during the summer particularly for brood females. If spruce grouse on POW Island are officially recognized as a subspecies and the birds are found to have unique old-growth preferences then there may be implications for the logging industry on Prince of Wales Island.

STUDY AREA

Located at 55° latitude and 132° longitude, POW in southeast Alaska is at the southern terminus of the Alexander Archipelago, approximately 10 miles from mainland Alaska (Fig. 1, Chapter 1). It is the third largest island in the U.S. at 6900 km^2 and is surrounded by hundreds of smaller islands of varying sizes. Deep fjords line the shore and the steep-sided Coast Mountains rise up to 1000 m in places. The climate is maritime and the island receives high levels of precipitation year-round (>250 cm). Winters are generally mild though large amounts of snow can fall at higher elevations. Summer temperatures are cool and autumn is typically the rainiest period of the year. Common bird species found on POW include willow ptarmigan (*Lagopus lagopus*), rock ptarmigan (*Lagopus mutus*), northern goshawk (*Accipiter gentilis*), sharp-shinned hawk (*Accipiter striatus*), northern saw-whet owl (*Aegolius acadicus*) and barred owl (*Strix varia*). Common mammals are marten (*Martes americana*), ermine (*Mustela ermine*), wolf (*Canis lupus ligoni*), black bear (*Ursus americana*), Sitka black-tailed deer (*Odocoileus hemionus sitkensis*), and POW flying-squirrel (*Glaucomys sabrinus griseifrons*). POW Island has a karst substrate which has resulted in a very productive forest system. Temperate rainforest characterizes the island with western redcedar (*Thuja plicata*), Alaska yellow cedar (*Chamaecyparis nootkatensis*), Sitka spruce (*Picea sitchensis*), western hemlock (*Tsuga heterophylla*), shore pine (*Pinus contorta var. contorta*), and red alder (*Alnus rubra*). Other plant species include Alaska blueberry (*Vaccinium alaskensis)*, red huckleberry (*Vaccinium parviflorum)*, crowberry (*Empetrum nigrum*), and bunchberry (*Cornus canadensis*), foam flower (*Tiarella trifoliate*) and five-leaved bramble (*Rubus pedatus*). The high productivity on POW Island supports a substantial amount of timber

harvest. POW Island is disproportionately logged compared to other areas in the Tongass with 41% of total harvest occurring on the island. Current forest management practices on the Island include clearcut logging, precommerical thinning, and creating gaps within second-growth canopy. Forest turnover rate for logging is expected at 60-80 years with the first second-growth harvest occurring in the next decade.

METHODS

Field Methods

During 2007 and 2008, we searched for spruce grouse throughout the relatively snow-free months of April to October. Grouse were captured with extensible noosing poles (Schroeder 1986, Zwickel and Bendell 1967) and fitted with Model 1550 4.5 g necklace-style radio transmitters from *Advanced Telemetry Systems, Inc.*, Isanti, MN. We radio-collared one bird per encountered brood and marked several chicks for the following field season. We confirmed breeding status of captured birds by searching for chicks and presence of a brood patch. We made an effort to recollar birds captured in 2007 for subsequent seasons.

We relocated grouse intensively ($\geq$1/month) from April -September 2007 and May-December 2008. We had limited success with triangulation accuracy; consequently, we visually monitored birds. For each encounter, we recorded geographic coordinates, behavior (brooding, nesting, foraging), habitat type, sign (feather/droppings), and position (on the ground, in a tree, on a nest). All relocations used were separated by at least one day. We varied relocation time among three periods of the day (morning,

afternoon, evening), but observation timing was contingent on tracking time, 30 minutes - 7 hours. Spruce grouse were also monitored during the off-season to identify over-winter habitat relationships and monitor survival.

Independent Variables

We used three habitat variables to examine potential effects of timber harvest on selection. 'Habitat' was a binary classification for either unharvested or harvested forest. Unharvested forest was forest was never harvested and also included muskeg and muskeg woodland while harvested forest is all ages of second-growth (inc. clearcuts) and commercially thinned second-growth. 'Distance to road' (m) was the distance to the nearest road, which can be open or closed and logging or paved. 'Distance to managed edge' (m) was the distance to the nearest edge associated with a harvest unit. This is the interface between unharvested and harvested forest and does not include edges created by roads through contiguous habitat. For breeding status we classified birds into either breeding or non-breeding states. A bird was in a breeding state if it was on a nest or attending chicks. Hens were classified as non-breeding if no chicks were confirmed, even if presence of a brood patch was detected; possibly selecting different habitats without the responsibility of chicks. Evidence of breeding was first detected on May 15, with the first nesting bird located. The latest documented dispersal of chicks was October 6. All males were assigned to the non-breeding category. For 'season' we considered differences between summer vs. winter. We classified summer on POW Island from 15 May to 6 October and winter as the remainder of the year.

Data Analysis

To determine which birds to include in the habitat selection analysis, we fitted a second-order polynomial to estimate the inflection point where number of observations did not affect homerange size. The inflection point was 16 observations, where further observations did not increase the maximum distance between relocations for a single bird. However, we did not have a sufficient sample size with 16 or more observations to conduct the analysis. Therefore, we used grouse with 10 or more observations (16 birds total) to estimate home range (Giesen and Braun 1992).

We used a use-availability design, where habitat selection is analyzed with respect to used and available locations to investigate 2nd (homerange in landscape) and 3rd (use in homerange) order selection (Manly et al. 1993, Johnson 1980). Available locations in this scenario can be comprised of both used and non-used points, however, use is likely rare (Manly et al. 1993), therefore, our data approximates a case-control study design (Keating and Cherry 2004). We used logistic regression to examine the relationship between habitat use and the five predictor variables described above. We used odds-ratios (Keating and Cherry 2004) to interpret habitat use as well as resource selection probability functions (Johnson et al. 2006). All data were analyzed using R-Project (R Development Core Team 2009). GIS data was provided by the USFS Thorne Bay Ranger District and The Nature Conservancy (Southeast Alaska GIS Library 2009).

To investigate 2nd order selection or the establishment of home range within a larger area, we delineated available habitat at the watershed level because we had no data that grouse emigrated out of a watershed and therefore selected habitat at a larger scale. More

specifically, we used the Alaska Department of Fish and Game Wildlife Analysis Area (WAA) classification system. WAA's are slightly smaller units than watersheds and are developed specifically for managing Alaska's game populations. We subsequently refer to WAA selection as watershed selection for interpretation. We randomly selected 100 points for each bird within the WAA in which it occurred. We did not sample in permanent water, ice, and rock habitats. For a bird whose homerange fell across the boundary of 2 WAA's, we generated 200 random locations, 100 for each WAA. The total number of points we included in 2nd order selection was 1904. We compared these to the observed relocations of grouse to see if home range selection was non-random.

To investigate 3rd order selection or areas of use within homerange (Johnson 1980), we estimated homerange using a maximum distance technique. Using individual relocations, we buffered a centroid with the greatest distance between points to create distinct home ranges for each bird. We delineated homerange into unharvested and harvested forest areas. We randomly selected 100 points within each homerange, excluding water, ice, and rock habitats. To investigate patterns of use we compared these random points to observed locations of grouse. The total number of points included in this analysis was 1804.

We developed a candidate model set where habitat selection was described as a function of habitat, breeding status, and time. We considered 33 biologically relevant models for each analysis. We assessed fit of the most general model in a set using the Hosmer-Lemeshow test (Hosmer and Lemeshow 1989). We examined the individual effect that habitat, distance to road, and distance to edge had on selection. We tested

additive models that were combinations of the above explanatory habitat variables and then incorporated breeding status and season. We tested models with interaction effects of breeding with habitat and distance to road; that the effect of roads on habitat use varied between breeding and non-breeding birds and that the effect of habitat type on habitat use also varied with breeding status. We used Akaike's Information Criteria adjusted for sample size (AICc) to select among competing models and only considered models with $\Delta AIC < 7$ to have adequate support in the data (Burnham and Anderson 2002). All variables were included using a logit link function.

RESULTS

WAA Analysis – 2nd order selection

Goodness-of-fit tests were not significant (16.78, p=0.03, α=0.01) indicating sufficient fit for the global model. The best approximating model (AICc weight = 1.0, Table 1) for second-order habitat use, included the effects of habitat, distance to road, distance to managed edge, breeding status, and season. The best approximating model was also the most complex model and the only model with any support in the data ($\Delta AIC \leq 7.0$, Table 1). For models that excluded one of the five variables in the best approximating model, there was essentially no support (AICc weight =~0.00).

Parameter estimates from the best approximating model show that spruce grouse used unharvested habitats at greater rates than harvested habitats, β_1=-0.716±0.2004. The relationship between use and distance to road was negative, β_2=-0.006±0.0006 and

between use and distance to managed edge was positive, β_3=0.001±0.0003. For both breeding and non-breeding birds use of harvested habitats was less than unharvested, β_4=-1.52±0.201, while use was higher near roads and lower near managed edges. These effects were more pronounced for non-breeding birds (Fig. 1). Similarly, in both winter and summer seasons, spruce grouse preferred unharvested habitat, short distances to roads, and greater distances to managed edges, β_5=1.68±0.204. However, these effects were more pronounced during the summer. In general, unharvested habitat, close proximity to roads, and greater distances to managed edges were preferred across breeding states and seasons.

At median distances from road (100.3 m) and managed edge (190.8 m), spruce grouse used unharvested habitats two times greater than harvested habitats across breeding status and season: $\beta_{0(\text{unharvested})}$=-0.554±0.2113 and $\beta_{0(\text{harvested})}$=-1.26 ±0.2912 (odds ratio: $0.4497_{(\text{unharvested})}/0.2198_{(\text{harvested})}$, Fig. 1). The probability of use for non-breeding birds in unharvested habitats is 0.46 while in harvested is 0.29. Breeding bird probability of use is 0.18 in unharvested forest and 0.09 in harvested forest. Summer use for non-breeding birds in unharvested forest is 0.62 and breeding birds is 0.29. In harvested forest during the summer, the probability of use for non-breeding birds is 0.44 and breeding is 0.17.

Within both unharvested and harvested areas, probability of use decreased at increasing distances from roads (Fig. 1). For both habitats, use was three times as high at 0.0 meters from road than at 200 meters from road across breeding status and season (odds ratio: $0.6611_{(0\text{ m road})}/0.2105_{(200\text{ m road})}$, at mean distance from edge). At 0.0 m road

in unharvested habitats, probability of use is 0.44 while in harvested it is 0.28. For non-breeding birds, use is 0.55 and for breeding use is 0.24. Probability of use at 200 m in unharvested habitats is 0.20 and 0.11 in harvested. For non-breeding birds, use is 0.28 and for breeding is 0.09.

Conversely, the relationship between use and managed edge was positive, with probability of use higher further from managed edges (Fig. 1). Spruce grouse were found 0-1800 meters from managed edge. For both habitats, probability of use was 10 times higher at 1,800 meters than 0.0 meters (odds $ratio_{(unharvested)}$: 3.5599/0.3517 and odds $ratio_{(harvested)}$: 1.7404/0.0.1719, at mean distance from road). This was also consistent for breeding and nonbreeding birds. At 0.0 m from managed edge probability of use for nonbreeding birds was 0.35 while it was 0.12 for breeding birds. At 1800 m managed edge, probability of use for nonbreeding birds was 0.84 and 0.59 for breeding birds.

Homerange Analysis – 3rd order selection

Goodness-of-fit tests were significant, indicating some lack of fit for the global model (29.66, p=0.0002, α=0.01). Results were very similar to those found with the 2nd order habitat analysis. The best approximating model included the effects of distance to road, distance to managed edge, breeding, and season (AIC weight=0.54, Table 2). There was approximately equivalent support (ΔAIC = 0.31) for a model that also included the effect of habitat (AIC weight = 0.46). These two models were the only models supported by the data (ΔAIC $\leq$ 7.0) and though there was similar support for both models, the more

complex model imprecisely estimated the variable habitat, with a 75% coefficient of variation.

Parameter estimates from the best approximating model show that the relationship between use and distance to road was negative, β_1=-0.004±0.0005 and between use and distance to managed edge was positve, β_2=0.002±0.0003. For both breeding and non-breeding birds use decreased with increasing distance from roads and increased with increasing distance to managed edge, β_3=-1.127±0.1806. This was also true during both summer and winter, β_4=1.145±0.1782.

At median distance from managed edge (190.8 m), both breeding and nonbreeding spruce grouse were two times more likely to be found at 0 meters from a road than 200 meters (odds ratio: 0.3950/0.1718, Fig. 2). Spruce grouse used roads equivalently during both summer and winter. Spruce grouse were found within 0-1800 meters of managed edge. Both breeding and non-breeding spruce grouse were 27 times more likely to be found in areas 1800 m from managed edges than 0 meters (at median distance from a road). The relationship between use and managed edges was equivalent during both summer and winter.

Spruce grouse are 2 times more likely to use areas that are within 0.0 m of a road as areas that are 200 m from roads, across breeding status and season: (odds ratio: $0.2362_{(0\text{ m road})}/0.1027_{(200\text{ m road})}$, Fig. 2). The probability of use for birds during summer at 0.0 m from road is 0.28 while during winter is 0.11. Birds found at distances of 200 m from the road had a lower probability of use during both summer, 0.14, and winter, 0.05. During the summer, non-breeding birds had a probability of use at 0.0 m road of 0.40 and 200 m

road 0.22. Breeding birds had a probability of use for 0.0 m road of 0.17 and 0.06 for 200 m road.

Spruce grouse are 27 times more likely to use areas that are at 1800 m from managed edges than 0.0 m from managed edges.: (odds ratio: $2.9572_{(1800\ m\ edge)}/0.1097_{(0\ m\ edge)}$). The probability of use for birds during summer at 0.0 m from edge is 0.15 while during winter is 0.05. At 1800 m from managed edge, the probability of use is 0.83 during the summer and 0.61 during the winter. During the summer, non-breeding birds had a probability of use at 1800 m edge of 0.89 and 0 m road 0.23. Breeding birds had a probability of use at 1800 m edge of 0.73 and 0.09 for 0 m edge.

DISCUSSION

Spruce grouse on mainland sites are found either in younger forests before canopy closure (Schroeder and Boag 1991) or in mature climax forests with strong horizontal diversity (Ratti et al. 1984). In general, the stem exclusion state produced by aging successional stands is not preferred, but the immediate regrowth following disturbance from logging or fire is used (Robinson 1969, Schroeder and Boag 1991).

We hypothesized that spruce grouse on POW would favor logging related openings, edges, and successional forest, which they are associated with on fire-influenced mainland sites. We found that logging appears to have direct negative and indirect positive consequences on habitat selection by spruce grouse on POW. Spruce grouse preferred unharvested forests and were less likely to be found near managed forest edges,

but were found in close association with roads, most of which were created to support logging activities.

Spruce grouse used harvested forest, but were much more likely to be found in unharvested forest. The negative effect of managed edge on selection suggests that spruce grouse need patches of contiguous habitat and are therefore classified as a core species (Huggard 2003). Avoidance of managed edge could be due to greater predation risk (Gates and Gysel 1978) and large amounts of restrictive blow down. Further, negative effects of edge could extend throughout the interior of the harvest unit creating another reason why this habitat is not preferred (Flaspohler et al. 2001). Conversely, grouse were positively associated with roads so there could be a sufficient edge effect that is conferred with road use. We documented grouse using roads to grit, travel, dust-bathe, and forage which is consistent for other species of grouse at mainland sites (Hollifield and Dimmick 1995, Whitaker et al. 2006). Ellison (1973) found that spruce grouse will travel upwards of 500 m to access roads. Roads could create favorable habitat and mitigate reductions in preferred habitat in this system.

Spruce grouse preference for areas adjacent to roads could be biased by the limitations of sampling on POW Island. Locating spruce grouse along the roadway proved to be the most effective method of increasing the encounter rate. The road system on POW is extensive across the northern half of the island. If we were to buffer these roads at 1 km, 59% of our study area would be comprised of these roads. With a 200 m buffer, 21% of the area is still affected. Consequently, it is difficult to quantify the effects of roads on

POW spruce grouse. We suggest that given the substantive infiltration of roads, our sample is a sufficient representation of the study area.

Clearcut logging and prescribed fire have been proposed as management techniques to create short-term habitat for spruce grouse (Ellison 1975, Schroeder and Boag 1991, Robinson 1969). On POW, spruce grouse did not respond positively to logging as they did to fire on mainland sites. Habitat disturbance on POW resulting from logging may lead to favorable conditions immediately following perturbation. However, it can take hundreds of years for temperate rainforest to reach a climax community (Alaback 1982) with adequate structure to support preferred spruce grouse habitat. Positive short-term disturbance to this ecosystem may not be balanced by the general unavailability of and reduced preference for second-growth forest during its succession.

On POW, we predicted that grouse would have specific seasonal requisites and use unharvested and harvested forest at different rates to meet these requirements. There were consistent differences in use depending upon season and breeding condition. Summer and non-breeding spruce grouse had higher probabilities of use in each habitat as well as at all distances from roads and edges. Winter and breeding birds did not have higher use for any habitat characteristics that we explored. For example, breeding birds had lower use than non-breeding birds in both unharvested and harvested habitat. Consequently, there may be other factors that are predicting use during these periods. Variables that we did not consider, such as proximity to streams and elevation, may be important during winter or for breeding birds. Proximity of streams could provide an available supply of grit during the winter when this resource is generally limiting and

broods could also find streams a convenient and safer source of grit during the summer. Also, there may be an elevation effect that influences seasonal selection such as winter preference for higher areas. Both could subtly interact with habitat in a manner that our dataset is not sensitive to. We briefly considered several models with interactions but in general did not investigate interactions due to limited sample size and difficulty in interpretation. In actuality, the relationship between use and habitat or distance to roads could differ depending upon whether or not a bird was breeding. Therefore the difference in habitat use between non-breeding and breeding birds or between summer and winter would not be due to some constant additive component.

In addition to interactions, it's possible that spruce grouse are able to find suitable denser or sparser habitat within unharvested forest. There are several structural features within unharvested forest that we did not investigate. These microhabitats include the Forest Service classified high-volume and medium-volume forests, scrub forest, muskeg woodland, and bog/muskeg. In fact, we documented broods using muskegs several times in our study. Similarly, the broader forest classification for harvested forest could mask seasonal selection for pre-commerically thinned areas or clearcuts. We documented broods using clearcuts several times, probably for berry foraging. Our data were not adequate to formally investigate selection at this small spatial scale and microhabitats may not be a realistic scale for management in the Tongass National Forest, where landscape level action is emphasized (Hanley et al. 2005).

Seasonal and brood selection for microhabitats could help explain our findings in the context of survival. For example, we did not detect differences in survival among habitat

types (Chapter 1) but found preferences for unharvested forest (Chapter 2). In addition, survival varied dramatically between breeding and nonbreeding birds but we did not find stronger brood habitat selection for any of the variables we considered. Further, there was no clear preference for specific habitats during winter but survival was highest during winter-spring. There are several explanations for these patterns. The first is that spruce grouse may have been selecting structural features at a finer scale than we analyzed and that there are advantages to seasonal selection of these microhabitats. In addition, spruce grouse on POW did not remain within a single habitat during a season and it could be that movements between unharvested and harvested forest is a strategy to maximize survival. We did not calculate transition probabilities or examine Markov processes; however, survival depending upon multiple states could be inherent in this system. Lastly, breeding bird survival is much lower regardless of the habitat they occupy. If breeding birds were selecting for a particular habitat, such as unharvested forest, their low survival could underestimate unharvested forest use, which is why we did not detect differences in harvest types.

Our study is the second investigation of habitat relationships of spruce grouse on POW Island. Russell (1999) also found that spruce grouse prefer unharvested forest. Specifically, grouse selected high-volume old-growth forest and muskegs while avoiding clearcuts. There was no evidence for seasonal habitat preferences. The results of that study were significant at the 3rd order of selection scale, or use of particular areas within a homerange (Johnson 1980). They did not find selection occurring at the level of homerange (2nd order selection) and concluded that data were too sparse to identify 2nd

order selection. Several methodological differences exist between the two studies. We used actual visual relocations of birds while Russell (1999) primarily used triangulations. Though some of Russell's (1999) findings corroborate our results, we suggest that the two studies have varying levels of resolution and are difficult to compare. Russell's (1999) study also included a much more limited portion of the island.

Spruce grouse on POW had stronger 2nd order than 3rd order selection. Stronger relationships at the watershed level emphasize homerange placement with respect to limited habitat on the island and territory overlap. Grouse place their homeranges in areas with access to large patches of contiguous old-growth habitat but that are within short distances to roads. Once their homerange is established, they may make more use of available habitats that include harvested forest.

Patterns of habitat use on islands that vary from mainland systems have not been well-documented. Grouse could respond differently to landscape alteration on islands for several reasons: climate, differences in habitat created by logging versus fire, or island dynamics. Islands typically have less variety of habitats and species richness; however, POW is an extremely large island so we suggest that climate and logging primarily influence habitat relationships. It's possible that harvest features do not provide a fitness advantage in association with continuous exposure to inclement weather. Furthermore, POW is a highly productive environment with rapid forest regeneration rates (Alaback 1982). The extremely thick regrowth in this system may vary from mainland sites so as to create less preferred habitat. Finally, logging tends to create forest with larger amounts

of abrupt edge (Harper et al. 2004) and completely eliminates the forest canopy while fire can leave sufficient canopy and has less edge per unit area (Imbeau et al. 1999).

On POW, there is no other landscape alteration besides logging that produces edges, openings, and successional forest to the scale of fire in the boreal forest. In an old-growth system, we propose that muskegs provide forest openings, edges are associated with habitat intergrades, and successional forest is sparsely distributed at riparian areas and windthrow events. Availability of these habitat features may be limiting for the grouse population on POW if logging does not create preferred habitat.

MANAGEMENT RECOMMENDATIONS

Spruce grouse were found in both unharvested and harvested habitats on POW. Though selection for unharvested forest was greater, managed edges and roads provide a clearer opportunity to formulate management actions. Reducing the edge associated with timber harvest by ensuring that there are large blocks of contiguous habitat may be beneficial to spruce grouse. In addition, our findings that spruce grouse prefer roads support earlier recommendations (Chapter 1) based on survival to use limited and temporary road closure in areas of high grouse use and at critical times for survival. Lastly, we suggest that POW spruce grouse habitat selection provides a frame of reference for how grouse may respond to habitat islands as future increases in logging and infrastructure development in the boreal forest are projected across the range of the spruce grouse.

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Table 1. Models and model selection results for 2nd order habitat use by spruce grouse on Prince of Wales Island, AK, USA, 2007-2009. Models are ranked according to Akaike Information Criterion, corrected for sample size (AICc). Models are presented with model weight (wi), model likelihood (L), and number of parameters in the model (k).

Model	AICc	ΔAICc	L	Wi	k
Habitat+D_Road+D_Medge+Breeding+SumWin	811.51	0.00	1.00	1.00	6
D_Road+D_Medge+Breeding+SumWin	822.73	11.22	0.00	0.00	5
Habitat+D_Road+Breeding+SumWin	830.88	19.37	0.00	0.00	5
D_Road+Breeding+SumWin	845.54	34.03	0.00	0.00	4
Habitat+D_Road+D_Medge+SumWin	862.79	51.28	0.00	0.00	5
Habitat+D_Road+D_Medge+Breeding	865.40	53.89	0.00	0.00	5
D_Road+D_Medge+SumWin	874.67	63.16	0.00	0.00	4
D_Road+D_Medge+Breeding	876.90	65.39	0.00	0.00	4
Habitat+D_Road+Breeding	884.07	72.56	0.00	0.00	4
Habitat+D_Road+SumWin	886.54	75.03	0.00	0.00	4
D_Road+Breeding	899.40	87.89	0.00	0.00	3
D_Road*Breeding	900.87	89.36	0.00	0.00	4
D_Road+SumWin	902.31	90.80	0.00	0.00	3
Habitat+D_Road+D_Medge	914.10	102.59	0.00	0.00	4
Habitat*D_Road	923.92	112.41	0.00	0.00	4
D_Road+D_Medge	927.60	116.09	0.00	0.00	3
Habitat+D_Road	937.75	126.24	0.00	0.00	3
D_Road	955.77	144.25	0.00	0.00	2
D_Medge+Breeding+SumWin	1147.32	335.81	0.00	0.00	4
Habitat+D_Medge+Breeding+SumWin	1149.03	337.52	0.00	0.00	5
Habitat+Breeding+SumWin	1194.42	382.91	0.00	0.00	4
D_Medge+Breeding	1196.11	384.60	0.00	0.00	3
Habitat+D_Medge+Breeding	1197.82	386.31	0.00	0.00	4
D_Medge+SumWin	1202.81	391.30	0.00	0.00	3
Habitat+D_Medge+SumWin	1204.32	392.81	0.00	0.00	4
Habitat+Breeding	1241.71	430.20	0.00	0.00	3
Breeding	1243.21	431.69	0.00	0.00	2
Habitat+SumWin	1249.91	438.40	0.00	0.00	3
SumWin	1250.91	439.39	0.00	0.00	2
D_Medge	1252.51	440.99	0.00	0.00	2
Habitat+D_Medge	1253.81	442.30	0.00	0.00	3
Habitat	1298.21	486.69	0.00	0.00	2
NULL	1298.60	487.09	0.00	0.00	1

+: additive relationship
*:interactive relationship
D_Road: distance to road
D_Medge: distance to managed edge
Habitat: 0=unharvested, 1=harvested
SumWin: seasonal classification for summer and winter
Breeding: breeding status where 0=nonbreeding and 1=breeding

Table 2. Models and model selection results for 3rd order habitat use by spruce grouse on Prince of Wales Island, AK, USA, 2007-2009. Models are ranked according to Akaike Information Criterion, corrected for small sample size (AICc). Models are presented with model weight (wi), model likelihood (L), and number of parameters in the model (k).

Model	AICc	ΔAICc	w_i	L	k
D_Road+D_Medge+Breeding+SumWin	1079.83	0.00	0.54	1.00	5
Habitat+D_Road+D_Medge+Breeding+SumWin	1080.15	0.31	0.46	0.85	6
Habitat+D_Road+Breeding+SumWin	1113.83	34.00	0.00	0.00	5
D_Road+Breeding+SumWin	1118.72	38.89	0.00	0.00	4
D_Road+D_Medge+SumWin	1121.82	41.99	0.00	0.00	4
Habitat+D_Road+D_Medge+SumWin	1122.53	42.70	0.00	0.00	5
D_Road+D_Medge+Breeding	1124.32	44.49	0.00	0.00	4
Habitat+D_Road+D_Medge+Breeding	1124.73	44.90	0.00	0.00	5
Habitat+D_Road+Breeding	1159.42	79.59	0.00	0.00	4
Habitat+D_Road+SumWin	1160.82	80.99	0.00	0.00	4
D_Road+D_Medge	1163.81	83.98	0.00	0.00	3
D_Road*Breeding	1163.92	84.09	0.00	0.00	4
D_Road+Breeding	1164.11	84.28	0.00	0.00	3
Habitat+D_Road+D_Medge	1164.72	84.89	0.00	0.00	4
D_Road+SumWin	1165.31	85.48	0.00	0.00	3
Habitat*D_Road	1175.42	95.59	0.00	0.00	4
Habitat+Breeding+SumWin	1182.42	102.59	0.00	0.00	4
D_Medge+Breeding+SumWin	1183.72	103.89	0.00	0.00	4
Habitat+D_Medge+Breeding+SumWin	1184.23	104.40	0.00	0.00	5
Habitat+D_Road	1203.41	123.58	0.00	0.00	3
D_Road	1207.31	127.47	0.00	0.00	2
Habitat+Breeding	1227.11	147.28	0.00	0.00	3
Breeding	1227.41	147.57	0.00	0.00	2
D_Medge+Breeding	1228.61	148.78	0.00	0.00	3
Habitat+D_Medge+Breeding	1228.92	149.09	0.00	0.00	4
SumWin	1233.11	153.27	0.00	0.00	2
Habitat+SumWin	1233.21	153.38	0.00	0.00	3
D_Medge+SumWin	1234.01	154.18	0.00	0.00	3
Habitat+D_Medge+SumWin	1234.72	154.89	0.00	0.00	4
NULL	1275.30	195.47	0.00	0.00	1
Habitat	1275.41	195.57	0.00	0.00	2
D_Medge	1276.31	196.47	0.00	0.00	2
Habitat+D_Medge	1277.01	197.18	0.00	0.00	3

+: additive relationship
*:interactive relationship
D_Road: distance to road
D_Medge: distance to managed edge
Habitat: 0=unharvested, 1=harvested
SumWin: seasonal classification for summer and winter
Breeding: breeding status where 0=nonbreeding and 1=breeding

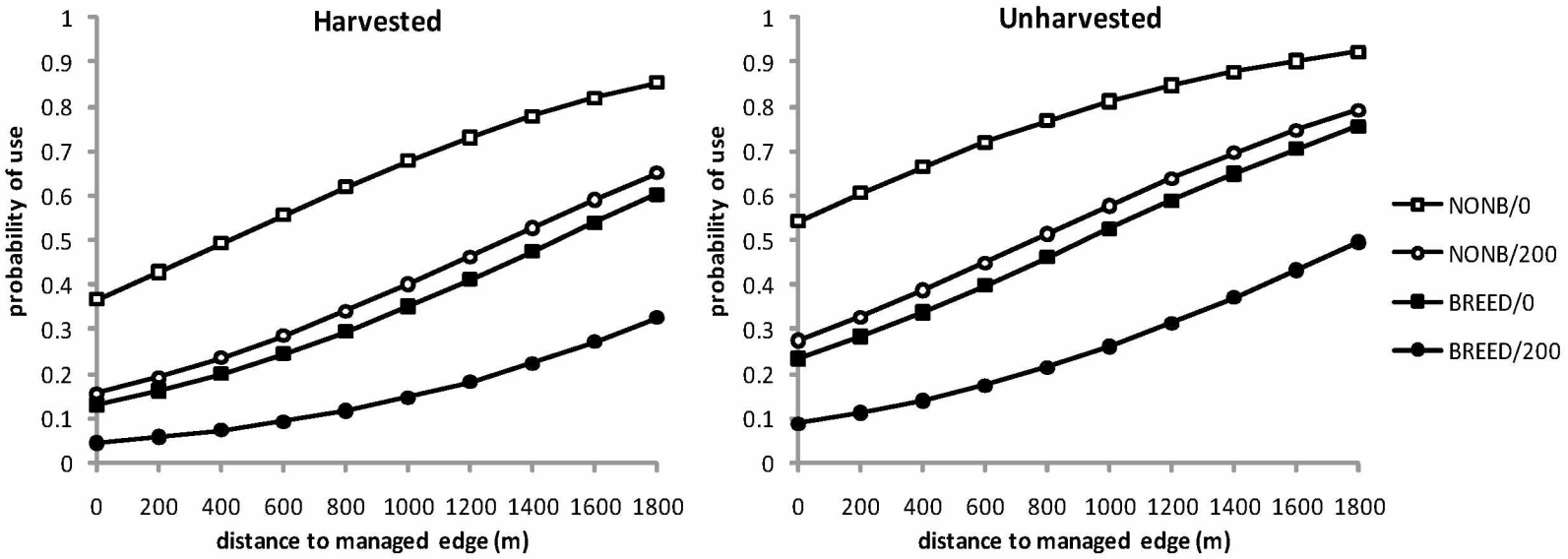

Figure 1. Relationship between probability of use for habitat and increasing distance from manged edge at varying distances from the road (m) for breeding (BREED) and nonbreeding (NONB) spruce grouse at the watershed level, Prince of Wales Island, AK, 2007-2009.

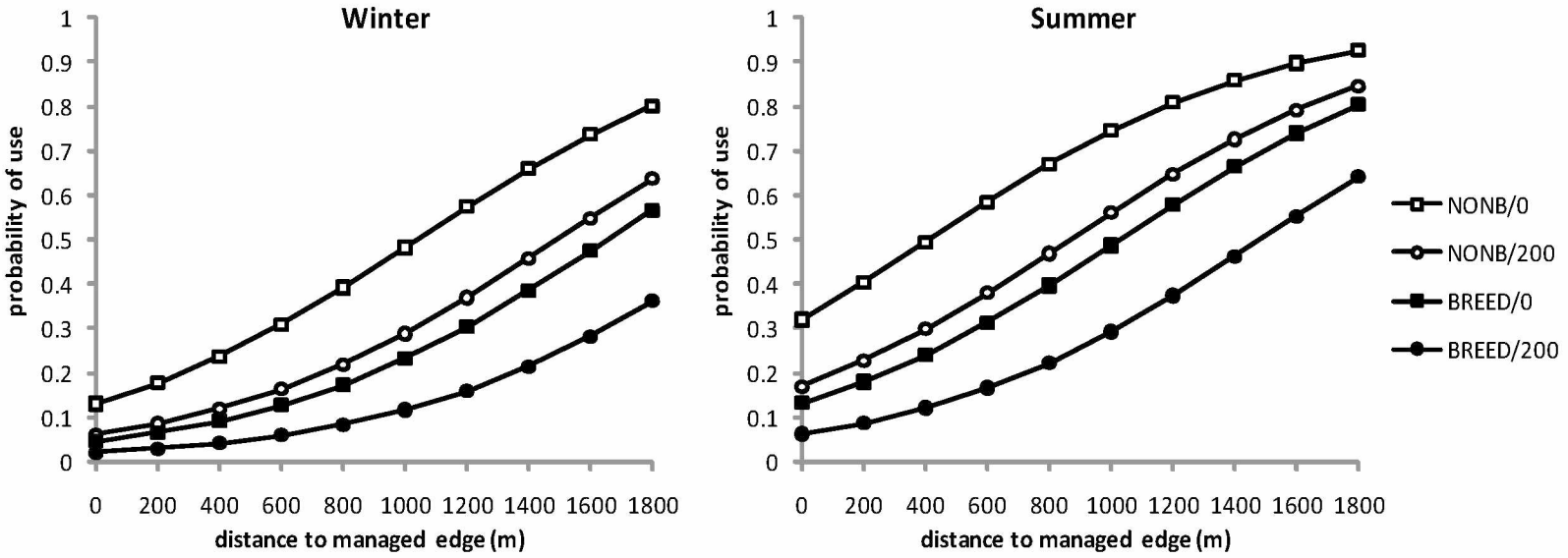

Figure 2. Relationship between probability of use for season and increasing distance from managed edge at varying distances from the road (m) for breeding (BREED) and nonbreeding (NONB) spruce grouse at the homerange level, Prince of Wales Island, AK, 2007-2009.

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CONCLUSIONS

Currently, there are no monitoring programs for grouse in Alaska that are linked to a decision framework for management. However, all upland bird species, including sharp-tailed grouse (*Tympanuchus phasianellus)*, blue grouse (*Dendragapus obscurus)*, ruffed grouse (*Bonasa umbellus)*, spruce grouse (*Falcipennis canadensis spp.)* and all three ptarmigan species (*Lagopus spp.*) are hunted. Relatively few studies have been conducted on grouse and ptarmigan in Alaska, particularly since the 1960's/1970's, and new documentation is required for effective management.

Information needs for grouse and ptarmigan primarily involve determining the status and distribution of populations as well as potential moderating factors such as fire and hunting. Currently, there is no reliable information concerning the abundance of grouse and ptarmigan populations in Alaska. In the past, determining abundance has relied upon harvest records and questionnaires regarding personal impressions of population fluctuations (Weeden 1965). Several roadside counts and ruffed grouse drumming surveys are in place, but these are not incorporated into population estimates.

Understanding the current status of grouse and ptarmigan may help to model how populations are influenced by changes in the future. Upland game birds in the arctic and alpine areas of Alaska may be particularly sensitive to the climate-related shifts in fire regimes and vegetation distribution that are projected for interior Alaska (Rupp et al. 2007, Euskirchen et al. 2009) due to their non-migratory habits. Fire in interior Alaska affects the habitats of spruce grouse, sharp-tail, and ruffed grouse and changes to fire frequency could alter mechanisms of population regulation.

In addition, the response of Alaska upland game birds to hunting pressure is relatively unknown. The degree to which roadside hunting affects local populations and the levels of recreational versus subsistence use are of interest (Weeden 1965). Further, it is unclear if hunting is compensatory in this system, though this is important for setting harvest quotas (Ellison 1991).

Alaska upland game bird management currently consists of static hunting regulations, which vary by game management unit but pool all grouse and ptarmigan species together. In addition, ruffed grouse were transplanted to the Matanuska-Susitna Valley, AK, and the Kenai Peninsula, AK, from 1988-1998 and prescribed burns to maintain ruffed grouse habitat on Nenana Ridge, AK, were conducted in 2005 and 2009. In other areas, such as northern Europe, upland game bird management involves active research into the role of hunting in population regulation (Steen and Erickstad 1996) and conservation of important habitats (Aberg et al. 2003). To effectively manage grouse and ptarmigan in Alaska, baseline information about their populations is required.

This study assists in meeting information needs for current grouse research and management in Alaska. In addition, there was a need for understanding the ecology of spruce grouse in temperate rainforest, particularly in light of proposals for subspecies classification (Dickerman and Gustafson 1996, Barry and Tallmon 2010) and current forest management practices. With this thesis, I sought to describe factors affecting the survival of spruce grouse on POW (Chapter 1), to determine habitat preferences (Chapter 2), and ultimately understand how timber harvest affects their ecology.

In Chapter 1, I conducted an analysis of survival rates of grouse. I expected that survival would vary with seasonal, sex, and breeding effects and predicted that there would be differences in survival rates of grouse associated with a particular habitat type. We hypothesized that grouse would have higher rates of survival during the winter and in harvested forest. Spruce grouse had the lowest survival during summer and fall and highest during a winter-spring. Large differences in survival were found between breeding and non-breeding birds but not between females and males. Annual estimates of survival for POW spruce grouse (0.39) are relatively low but still within the range reported for other subspecies of spruce grouse, 0.30 to 0.68 (Ellison 1974, Boag et al. 1979). However, the breeding season on POW Island may vary from other systems as we documented nesting activity from May 14 to July 1 and final dispersal October 6. Differences in the breeding season could be in response to a greater degree of climactic variability in maritime southeast Alaska. Survival rates did not vary between unharvested and harvested forest, therefore, we used causes of mortality to make management recommendations.

I also detailed our findings for the development of a sampling technique for POW spruce grouse in Chapter 1. Driving surveys yielded the highest number of encounters, but these were highly impacted by weather and type of road (logging or paved). We recommend using our findings to shape subsequent methods. Future work surveying POW spruce grouse should consider the unavailable component (i.e. birds in trees, Thompson 2004) of the population and we suggest selecting a time of year when birds on the ground (berry season or breeding season) to find spruce grouse.

In Chapter 2, we examined 2nd and 3rd order habitat selection (Johnson 1980) of POW spruce grouse in response to timber harvest. We predicted that spruce grouse would use certain harvest features, particularly edge habitats, in a manner in which they use opening, edges, and successional forest created by fire in mainland habitats. In the absence of fire within temperate rainforest, timber harvest is the only landscape-altering factor that creates edge habitat to the extent that fire does in the boreal forest. We found that spruce grouse prefer unharvested forest to harvested forest. Spruce grouse still use harvested forest but selection for unharvested forest is three times greater at the watershed scale. There was no support for the hypothesis that spruce grouse use harvest features similarly to fire features. Most studies have found that spruce grouse prefer early successional forest (Boag and Schroeder 1992). Patterns of habitat selection on POW appear to be different from spruce grouse in other systems.

POW spruce grouse represent a relatively unstudied population of spruce grouse. In addition, they also present the opportunity to investigate how island populations, particularly within temperate rainforest, may differ from mainland populations. This could be applicable to studies of grouse ecology in habitat islands within larger environments and in regions with occurring or expected landscape alteration. To this end, there are several areas for future spruce grouse research that are interesting from ecological and management perspectives. Currently, there is no information regarding productivity, fledging rates, dispersal, and recruitment for POW spruce grouse. We determined that breeding birds had the lowest rates of survival. Given the degree to which breeding bird survival is impacted by this environment, it is possible that other

population parameters related to breeding are also negatively affected. Grouse chick survival is often influenced by weather conditions (Erickstad 1985) and this may be a regulatory factor of grouse in temperate rainforest where wet conditions are prevalent.

We documented multiple long distance movements (~1 km) that occurred within short-intervals of one day to one week throughout the year. Spruce grouse are typically viewed as sedentary birds (Boag and Shroeder 1992), but short migrations (typically 1.5km – 5km) between wintering and breeding ranges occur in portions of populations (Herzog and Keppie 1980). It is possible that greater daily movements on POW are in response to pressure from predators, interactions with conspecifics, or are habitat driven. More research is needed to determine why spruce grouse are moving in this manner.

Though managing at the level of microhabitat may not be possible in the Tongass National Forest, we suspect that spruce grouse are using structure within unharvested and harvested forest and that this may vary seasonally. The degree to which muskegs, high-volume forest, riparian areas, clearcuts, different ages of second-growth, and precommerically thinned areas are used or selected for is unknown. Russell (1999) found that spruce grouse select for high-volume old-growth and muskeg habitats while avoiding clearcuts. Spruce grouse also used second-growth forest in proportion to availability (Russell 1999). We documented spruce grouse in each of these habitats and believe that a finer scale study of subhabitats would reveal seasonal habitat selection for these specific areas (Boag and Schroeder 1992).

Lastly, the abundance of spruce grouse is unknown on POW Island. Our attempts to develop a survey technique to reliably find birds had limited success. To yield higher

encounter rates in the future, I suggest using results on habitat preferences to direct searching for grouse. Future researchers may be more effective if they apply sampling techniques developed thus far to survey areas with higher probability of occurrence. Ultimately, an efficient sampling technique will aid in determining POW spruce grouse population size and conservation status. Small isolated populations are particularly sensitive to both demographic and environmental stochasticity (Lande 1993). To assess extinction risk of this differentiated population would require estimates of abundance to model how they respond in isolation to changes in their environment.

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APPENDIX

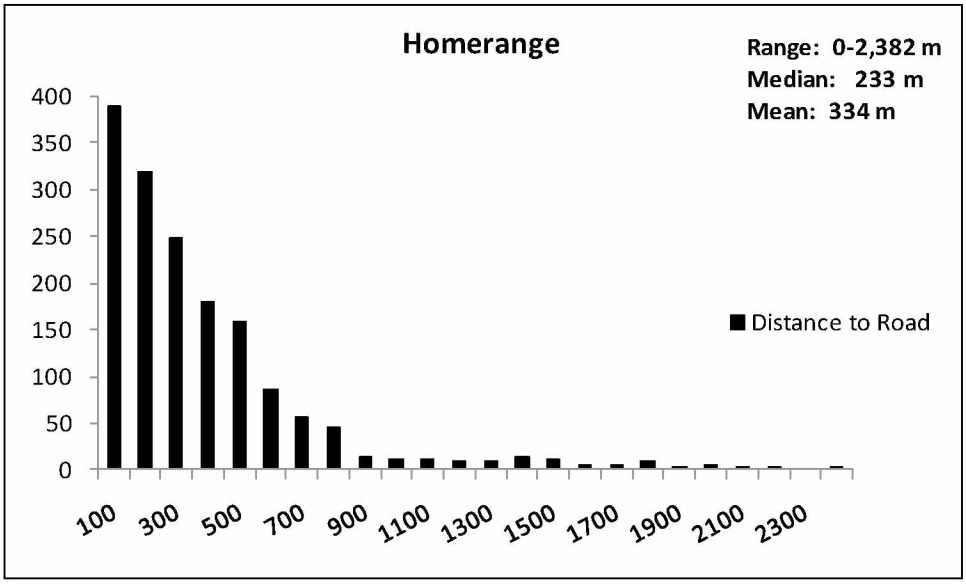

Figure 1. Random point distribution at the homerange level for variable distance to road, Prince of Wales Island, Alaska, 2007-2009.

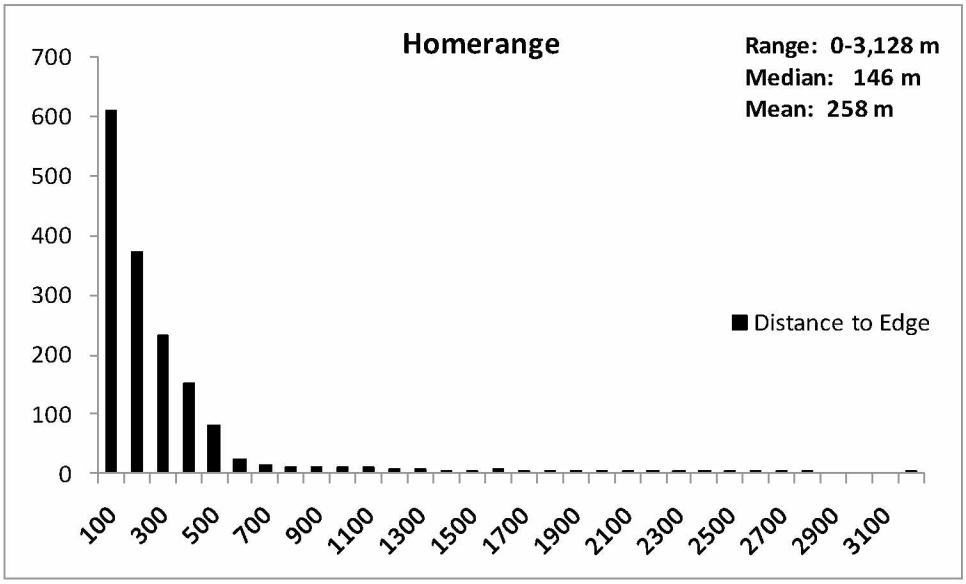

Figure 2. Random point distribution at the homerange level for variable distance to managed edge, Prince of Wales Island, Alaska, 2007-2009.

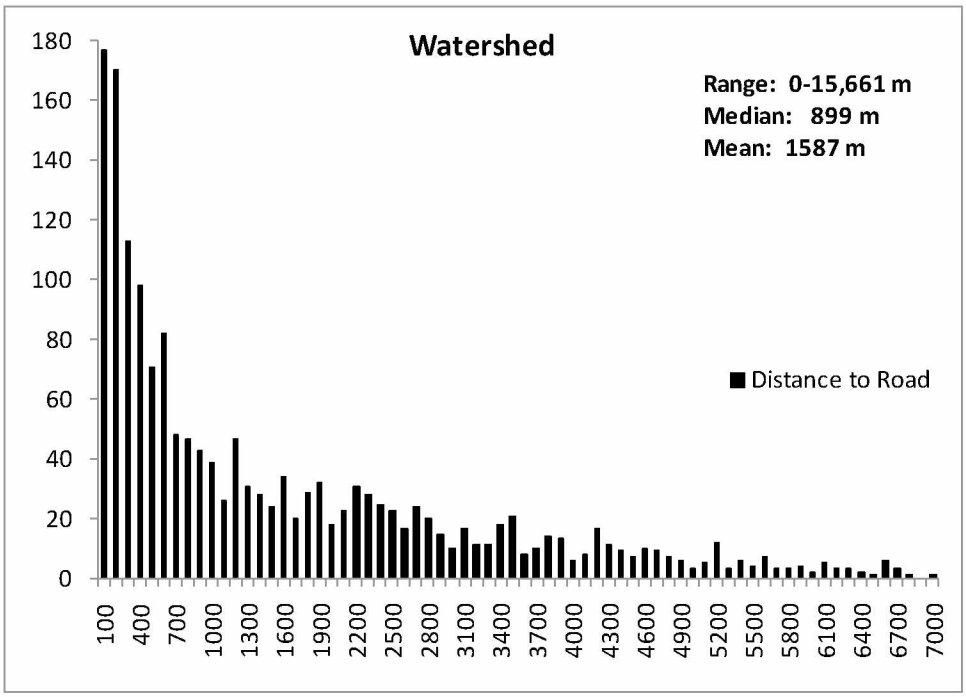

Figure 3. Random point distribution at the watershed level for variable distance to road, Prince of Wales Island, Alaska, 2007-2009.

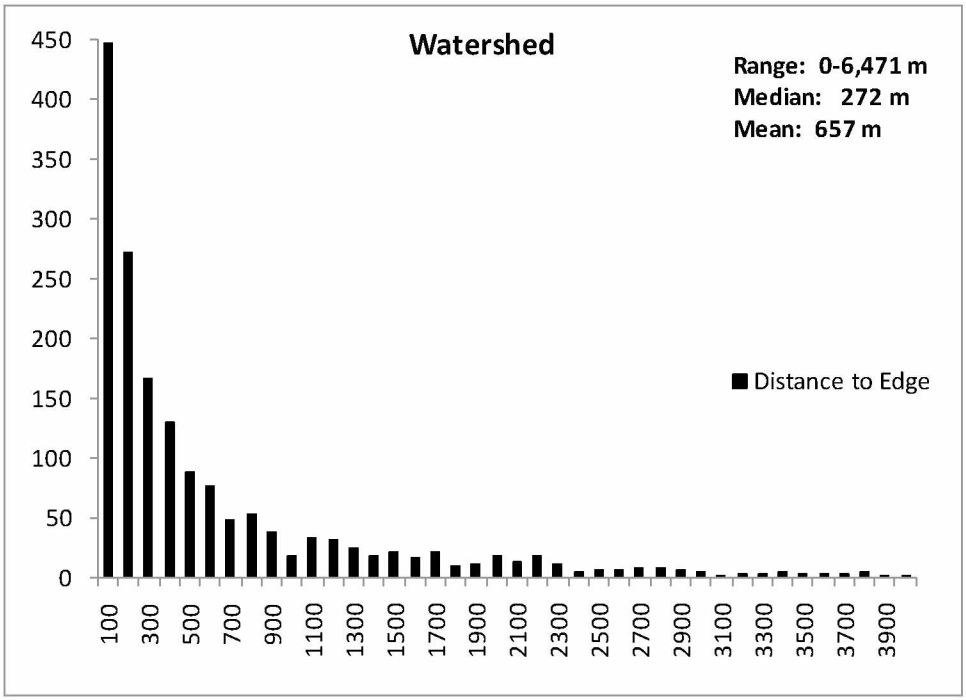

Figure 4. Random point distribution at the watershed level for variable distance to managed edge, Prince of Wales Island, Alaska, 2007-2009.

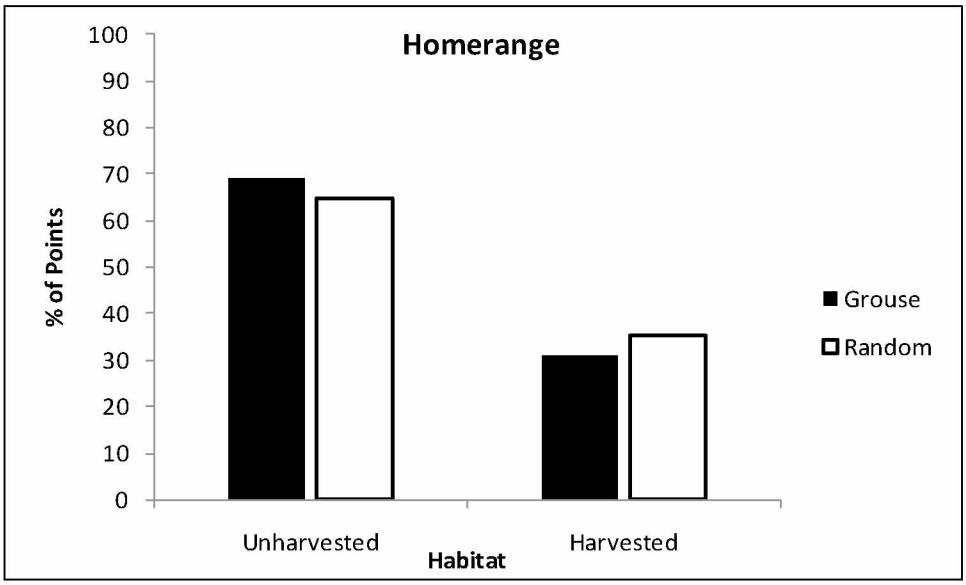

Figure 5. Histogram of proportion of points occurring in each habitat type for homerange analysis, Prince of Wales Island, Alaska, 2007-2009.

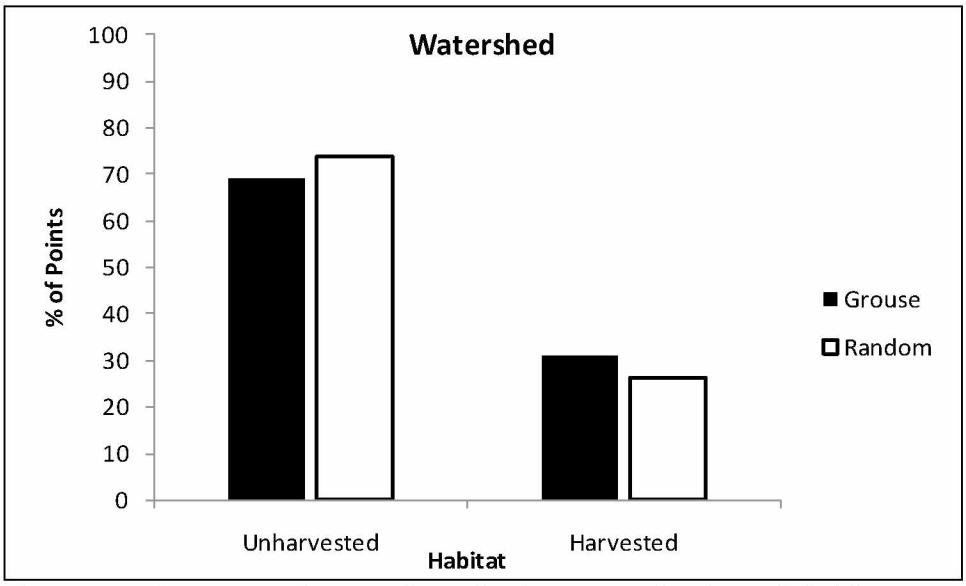

Figure 6. Histogram of proportion of points occurring in each habitat type for watershed analysis, Prince of Wales Island, Alaska, 2007-2009.

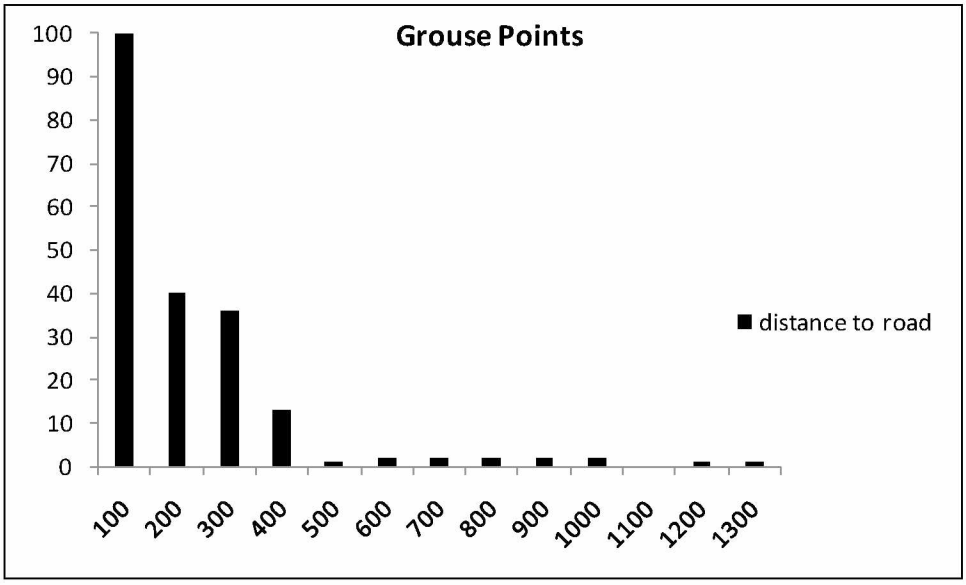

Figure 7. Histogram of points occurring at interval road distances (m) for actual grouse relocations, Prince of Wales Island, Alaska, 2007-2009.

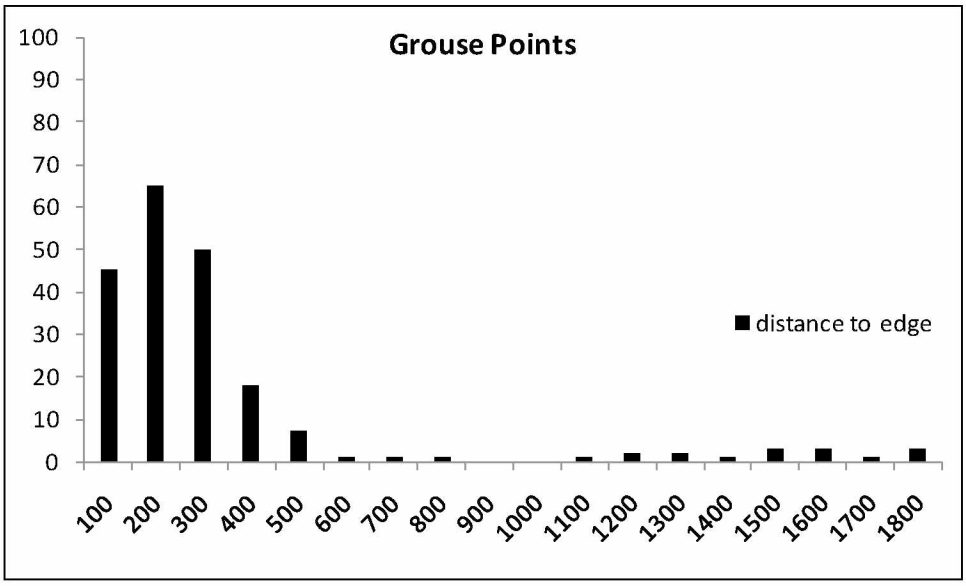

Figure 8. Histogram of points occurring at interval edge distances (m) for actual grouse relocations, Prince of Wales Island, Alaska, 2007-2009.

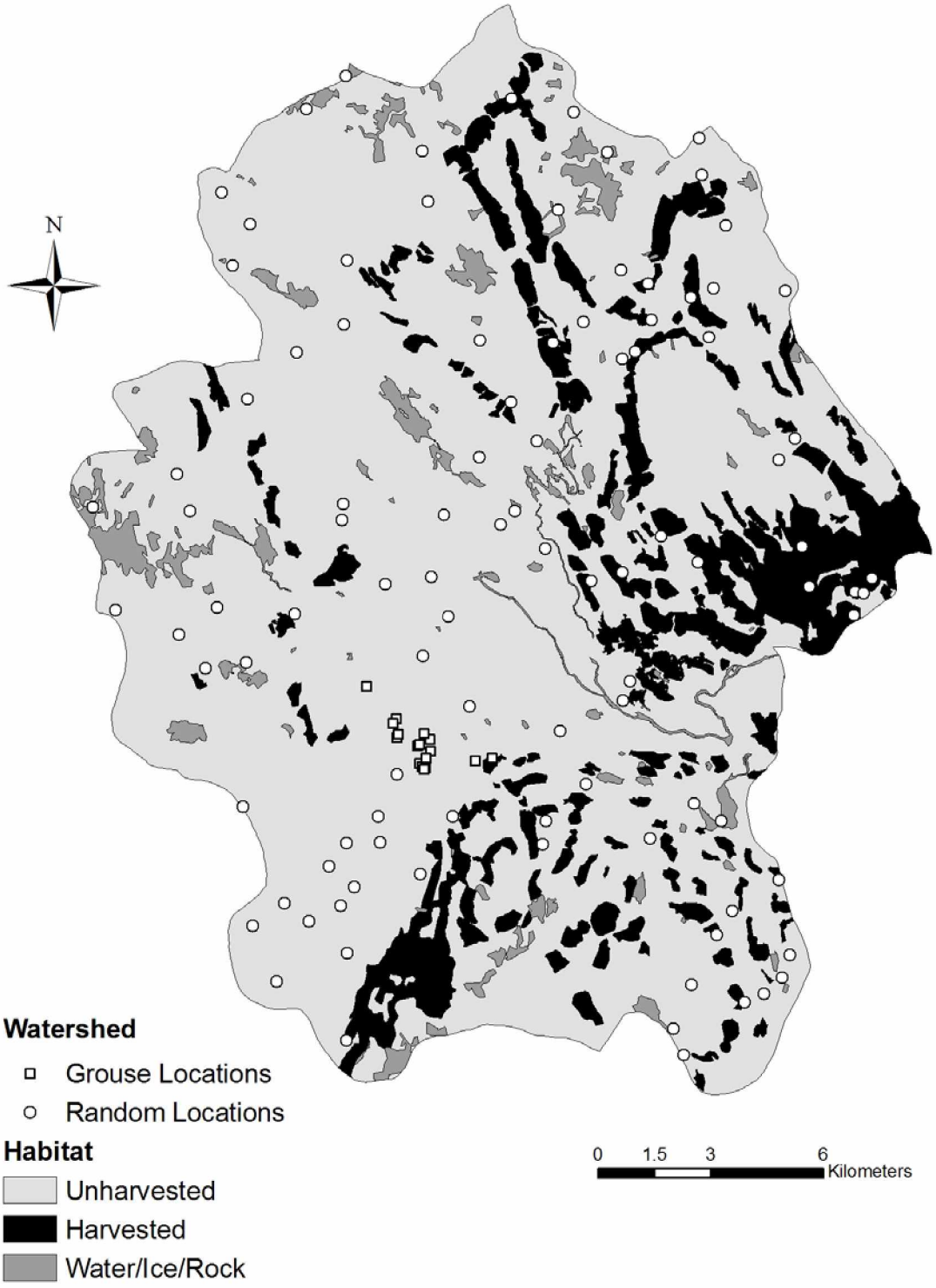

Figure 9. Watershed habitat delineation showing actual grouse locations and random selection of available locations, Prince of Wales Island, Alaska, 2007-2009.

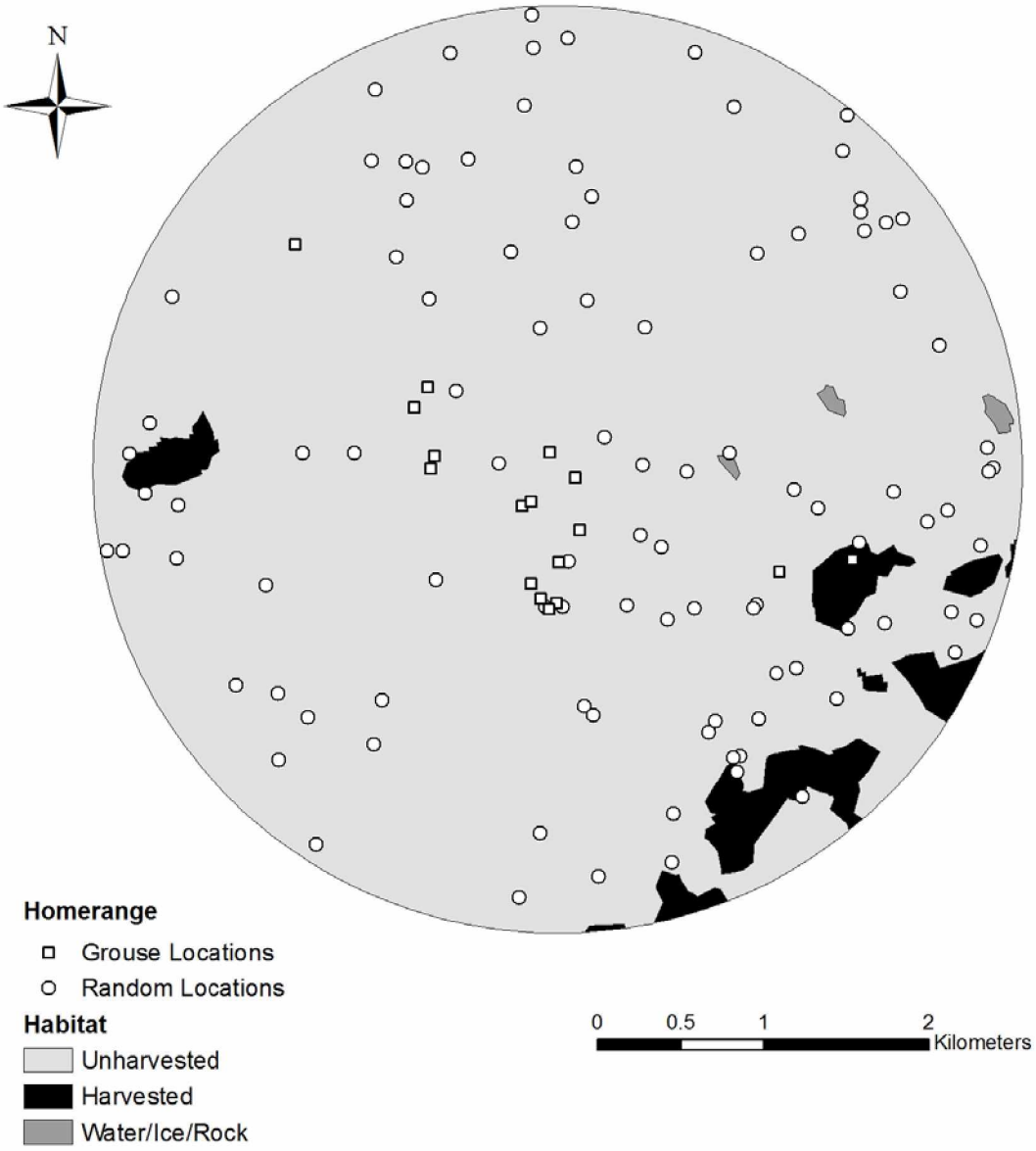

Figure 10. Homerange habitat delineation showing actual grouse locations and random selection of available locations, Prince of Wales Island, Alaska, 2007-2009.

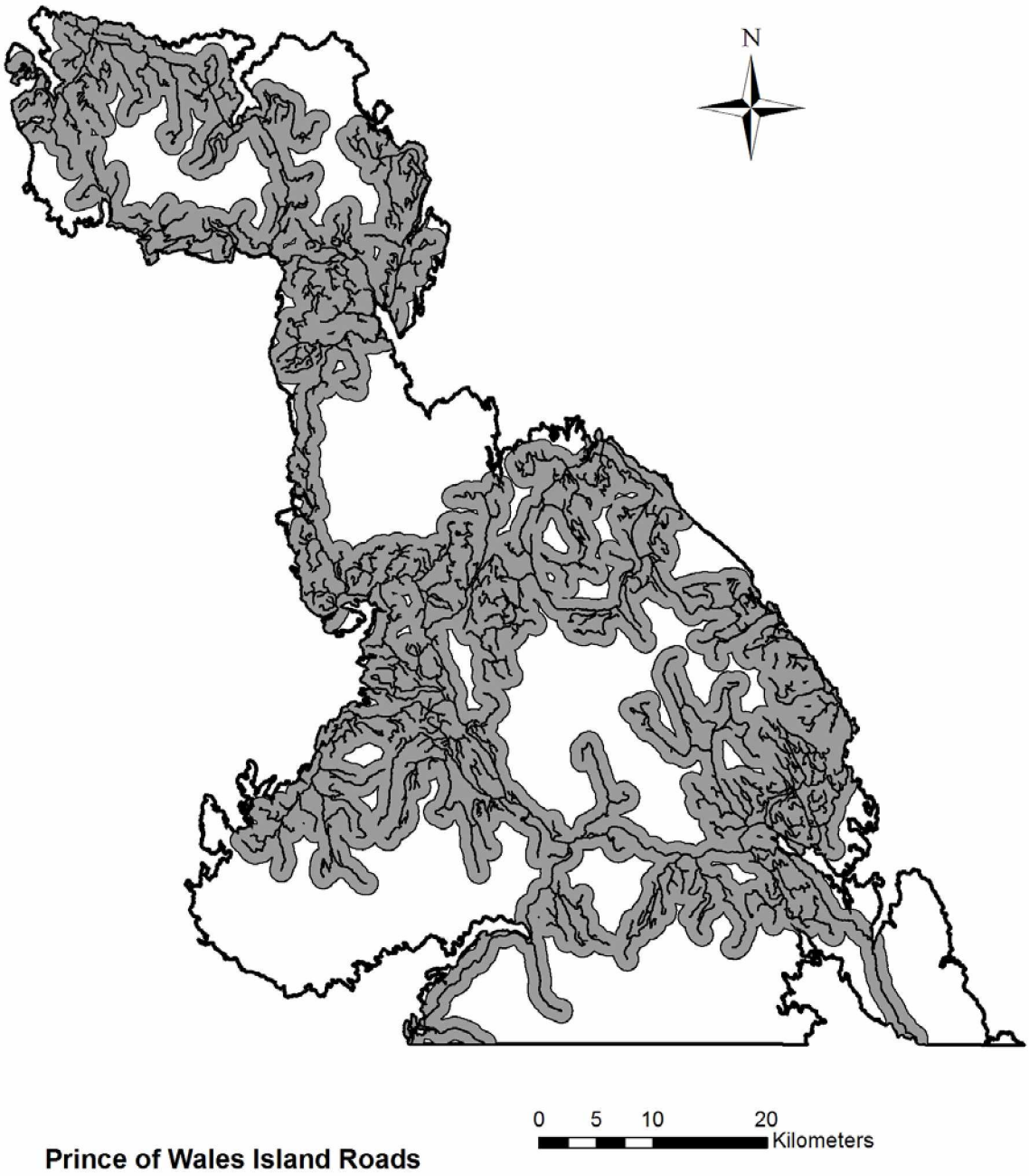

Figure 11. Northern portion of POW Island showing road system and 1 km buffer, equivalent to 59% of area, Prince of Wales Island, Alaska, 2007-2009.

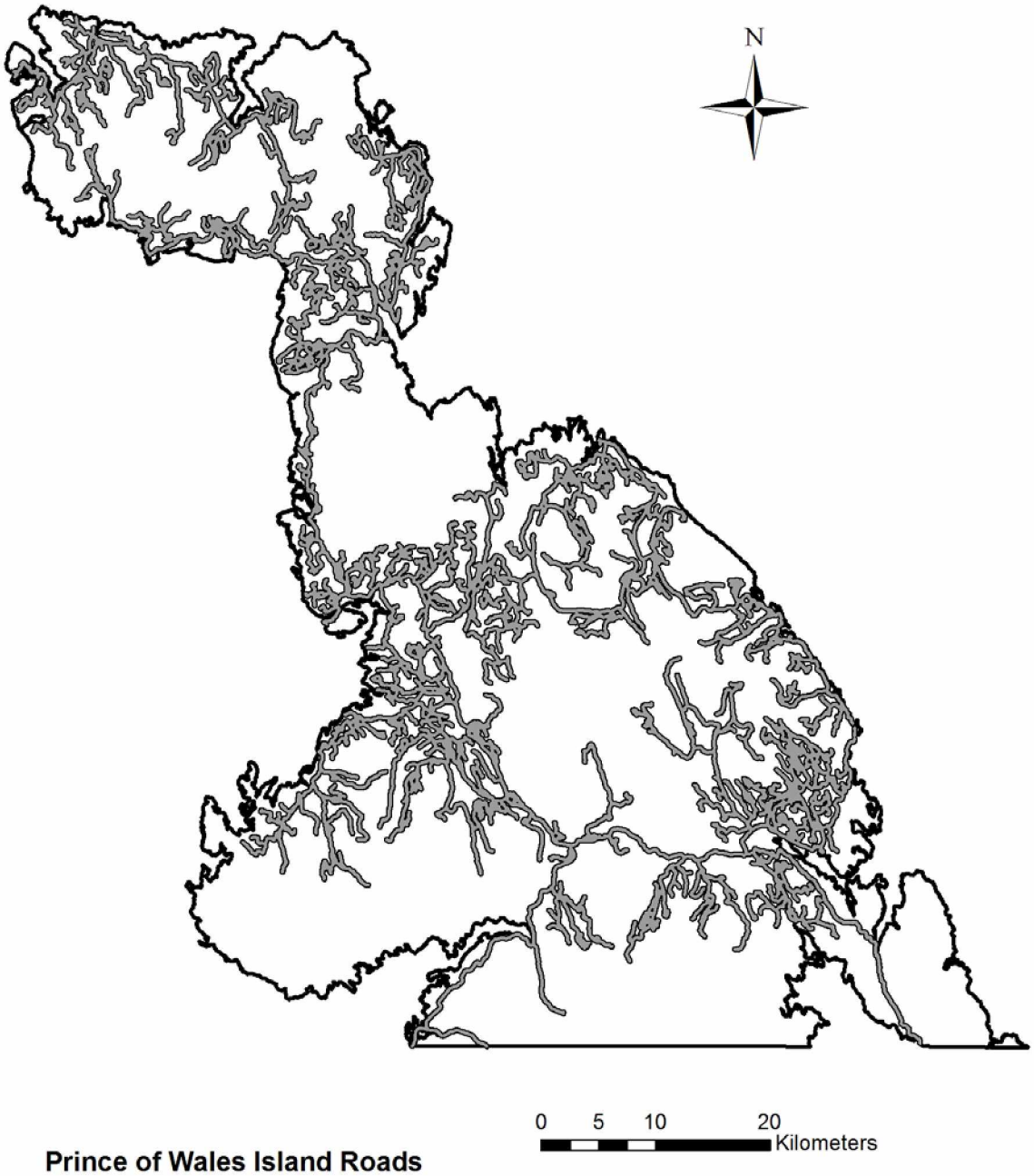

Figure 12. Northern portion of POW Island showing road system and 200 km buffer, equivalent to 20% of area, Prince of Wales Island, Alaska, 2007-2009.